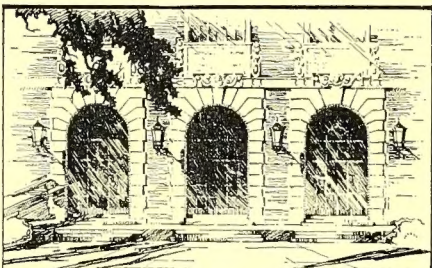


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STUDIES ON GREGARINES II

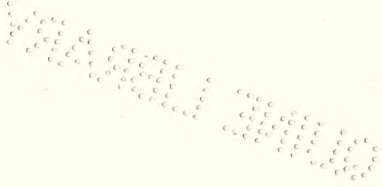
SYNOPSIS OF THE POLYCYSTID GREGARINES
OF THE WORLD, EXCLUDING THOSE
FROM THE MYRIAPODA,
ORTHOPTERA, AND
COLEOPTERA

WITH FOUR PLATES

BY
MINNIE WATSON KAMM

Contributions from the
Zoological Laboratory of the University of Illinois
under the direction of Henry B. Ward, No. 195

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INTRODUCTION

This monograph constitutes the second half of a problem in which it is endeavored to bring together in small compass the more important facts concerning the systematic position of polycystid gregarines. The first part of the work (Watson, 1916a) was published in 1916 and included the polycystid gregarines recorded from the Coleoptera, Orthoptera, and Myriapoda of the world. The present paper comprises those from the remainder of the animal kingdom. It is designed chiefly for the use of workers on gregarines who do not have access to the vast literature which has developed upon the subject and with which the University library is so richly endowed.

I wish to thank Professor Henry Baldwin Ward for kindly encouraging the publication of this paper, for his advice and judgment concerning some of the knotty systematic questions involved, and for the use of the laboratory and library facilities in his Department.

When the first paper was published Dr. C. W. Stiles, of Washington, informed me concerning the desirability of designating the type species of the various genera, and this has been done in the present paper. He also gave his opinion concerning the type species of the genus *Cephaloidophora*, for which I wish to express my thanks.

The larger groupings used in the present paper are made from the standpoint of the host-material rather than the parasite itself in order to facilitate work in the field. From the descriptions it can be at once determined whether or not a particular gregarine has ever been found in identical or similar material. If it has not been described from hosts in the same group and its position is definitely established from some one or more of the generic characters, one may turn to the index of this and of the preceding paper, where all the known species in each genus are ranged in alphabetical order under the generic name. From a comparison of all the known species with the species in hand it may be determined whether or not the latter has been described from some other group. It is true, however, that except in rare instances a species is confined to a single host or to nearly-related hosts, not being found in insects as far removed from each other as the Coleoptera and the Orthoptera.

In this paper I have not tabulated a complete alphabetic list of the gregarine genera with their hosts or of the hosts with their parasites for this reason: Two such lists were given in the former paper covering the species

up to 1915, and those described since then are listed in the same manner at the end of the present paper.

The previous monograph covers the species known from the Coleoptera, Orthoptera, and Myriapoda up to the year 1915. The gregarines parasitic in the remainder of the animal kingdom up to the beginning of 1920 are described in the present work. The arrangement of hosts in orders and classes of the Hexapoda follows that given by Comstock (1912).

Because more and more species are being described in such great genera as *Gregarina*, *Actinocephalus*, etc., which are very similar in all their characteristics but yet are distinct species, I believe accurate and detailed measurements are necessary for the sporonts, trophozoites, cysts, and spores, or as many of these characters as may be determined. Measurements should be made of quiescent but not water-swollen animals while alive on the slide. These measurements must needs be made very quickly after the host is opened for a water medium is highly destructive to the ectosarc of the gregarine, at first causing it to swell out of all normal proportions and then to break, with the collapse of the animal. When the parasites do not die within a short time (e.g., the *Stenophoridae*) they at least lose their original proportions and measurements become valueless. Those taken on preserved material are far from accurate.

Ratios used in this paper indicate length of protomerite to total length (LP:TL) and width of protomerite to width of deutomerite (WP:WD) as indicated in the author's drawings even though no measurements may have been made.

One would like to make a clean-cut and sweeping statement that polycystid gregarines are parasites of the arthropods exclusively and unless an exhaustive study be made this may seem to be true.

But just as higher animals cannot be placed under such definite groups, so it is with these simply organized forms. There is a gradual transition from simple to complex—from the unilocular to the septate forms, and from the simpler to the higher septate organisms. As shown in the group of tables in this paper, I believe there is an interesting and not entirely imaginary parallelism in the character of the hosts which harbor these developing parasites. The transitional forms between non-septate and septate gregarines are found exclusively in the polychaetes. The two lowest (and very similar) families of septate gregarines are found in lowly organized arthropods—the Crustacea and Diplopoda. These gregarines possess no epimerites or very rudimentary ones.

The next higher family, in which the epimerite is a very simple structure, is abundantly represented in the Orthoptera, but also in the Coleoptera (which is not one of the lower orders), and is fairly general throughout the Hexapoda. Just as the line of evolution in higher animals may take a single track however aberrant it may prove to be, this is apparently

true in gregarines, for many instances may be mentioned in which genera are found exclusively in a single order of insects; the genus most frequently present in the Acerata (Sciadophora) is found nowhere else and is highly specialized and unique along a particular line.

A gregarine has even been found in *Peripatus*; and the Tunicates contain true septate forms. It would be interesting to know what becomes of these parasites above the Tunicates—whether they lose their gregarinoid and take on higher characteristics, continuing to develop in vertebrates, or whether the alimentary tract of the latter contain enzymes not suited to their continued existence and they are thereby extinguished.

A suggested problem is that of the possibility of the existence of gregarines in the insects found in Baltic amber; the insects being transparent their presence or absence should be easily determined, and possibly some of the generic characters.

CLASSIFICATION OF THE TRIBE CEPHALINA

WITH THE TYPE SPECIES

Order 1. Gregarinoidea Minchin 1912.

Suborder 1. Eugregarinae Léger 1900.

Tribe 1. Cephalina Delage and Hérouard 1896 (Intestinal parasites almost exclusively).

Family 1. Lecudinidae Kamm 1922. Non-septate gregarines inhabiting digestive tract of polychaetes. Epimerite a simple knob.

Genus 1. *Lecudina* Mingazzini 1891:469. Non-septate, epimerite simple, spores ovoidal with thickening at one pole.

Type: *Lecudina pellucida* (Kölliker) Mingazzini.

Family 2. Polyrrhabdinidae Kamm 1922. Septate gregarines inhabiting the digestive tract of polychaetes. Epimerites varied.

Genus 2. *Polyrrhabdina* Mingazzini 1891:229. Septate, sporonts flattened, ovoidal, epimerite a corona of hooks. Intestine of polychaetes of the family Spionidae.

Type species: *Polyrrhabdina spionis* (Köll.) Ming.

Genus 3. *Sycia* Léger 1892:52. Epimerite knobbed, bordered by a thick ring. Protomerite subspherical, deutomerite conical with many inclosures in adult.

Type: *Sycia inopinata* Léger.

Genus 4. *Ulivina* Mingazzini 1891:235. Elongate-ellipsoidal, protomerite the more dense.

Type: *Ulivina elliptica* Ming.

Family 3. Cephaloidophoridae Kamm 1922. Sporonts associated in twos, no epimerite. Development intracellular; cyst dehiscence by simple rupture, spores ovoidal with equatorial line. Parasites of Crustacea.

Genus 5. *Cephaloidophora* Mawrodiadi 1908:101. Characters of the family.

Type: *Cephaloidophora communis* Mawrodiadi.

Family 4. Stenophoridae Léger and Duboscq 1904:361. Sporonts solitary, epimerite absent or rudimentary. Development intracellular; cyst dehiscence by simple rupture, spores ovoidal with equatorial line. Confined to Diplopods.

Genus 6. *Stenophora* Labbé 1899:15. Characters of the family.

Type: *Stenophora juli* (Frantz.) Schn.

Genus 7. *Fonsecaia* Pinto 1918:?. Like type genus except spores elongate-ellipsoidal, no endospore.

Type: *Fonsecaia polymorpha* Pinto.

Family 5. Gregarinidae Labbé 1899:9. Epimerite symmetrical, simple. Sporonts solitary or in association. Cysts with or without spore-ducts, spores symmetrical. (Confined to insects with two exceptions, development extracellular.)

Genus 8. *Leidyana* Watson 1915:35. Sporonts solitary, epimerite a simple sessile knob. Dehiscence by spore-ducts. Spores barrel-shaped, in chains.

Type: *Leidyana erratica* (Crawl.) Wats.

Remarks in parenthesis are added by the writer.

- Genus 9. *Gregarina* Dufour 1828:366. Sporonts associated in twos, epimerite a simple globular or cylindrical papilla. Cysts with spore-ducts, spores barrel-shaped, extruded in chains.
Type: *Gregarina ovata* Duf.
- Genus 10. *Protomagalhãensia* Pinto 1918: ? Sporonts in associations of several individuals, often attached laterally. Myonemes prominent. Sporonts attenuate. (Cysts and epimerites unknown.) Spores barrel-shaped, spine at each corner.
Type: *Protomagalhãensia serpentula* (Magal.) Pinto.
- Genus 11. *Gamocystis* Schneider 1875:587. Protomerite only in trophozoite, sporonts in twos; sporulation partial, with spore-ducts, spores cylindrical.
Type: *Gamocystis tenax* Schn.
- Genus 12. *Hyalospora* Schneider 1875:583. Sporonts in associations of two, endoplasm yellow-orange. Epimerite a simple globular knob.* Cyst dehiscence by simple rupture, spores ellipsoidal.
Type: *Hyalospora roscoviana* Schn.
- Genus 13. *Hirmocystis* Labbé 1899:12. Sporonts in associations of from two to twelve (or more). Epimerite a small cylindrical papilla. Cysts spherical, dehiscence by simple rupture, spores ovoidal.
Type: *Hirmocystis ventricosa* (Léger) Labbé.
- Genus 14. *Euspora* Schneider 1875:582. Sporonts in twos. (Epimerite unknown.) Cysts spherical, dehiscence by simple rupture, spores prismatic.
Type: *Euspora fallax* Schn.
- Genus 15. *Sphaerocystis* Léger 1892:115. Protomerite only in trophic stages, sporonts solitary, subspherical. Cysts spherical, dehiscence by simple rupture, spores ovoidal.
Type: *Sphaerocystis simplex* Léger.
- Genus 16. *Cnemidospora* Schneider 1882:446. Sporonts solitary, anterior half of protomerite gray, posterior half yellow-green. (Epimerite not known.) Cyst dehiscence by simple rupture, spores ellipsoidal.
Type: *Cnemidospora lutea* Schn.
- Genus 17. *Uradiophora* Mercier 1912:198. Sporonts in twos, deutomerite with small appendix. Epimerite an elongate papilla. Cysts ovoidal, dehiscence by simple rupture, spores spherical or subspherical, extruded in chains. Development extracellular.
Type: *Uradiophora cuenoti* (Merc.) Merc.
- Genus 18. *Pyxinoïdes* Trégouboff 1921: liii. Sporonts in associations of two, epimerite a slightly stalked globular papilla with sixteen longitudinal furrows, small cone at apex. Extracellular development.
Type: *Pyxinoïdes balani* (Köll.) Trég.

- Family 6. Didymophyidae Léger 1892:105. Sporonts in associations of two or three. No septum in satellites.
- Genus 19. *Didymophyes* Stein 1848:186. Epimerite a small pointed papilla. Cysts spherical, dehiscence by simple rupture, spores ellipsoidal.
- Type: *Didymophyes gigantea* Stein.
- Family 7. Actinocephalidae Léger 1892:166. Sporonts solitary, epimerites complex and varied. Cyst dehiscence by simple rupture, spores irregular, biconical, or cylindro-biconical. (Practically confined to insects.)
- Genus 20. *Amphoroides* Labbé 1899:20. Protomerite cup-shaped, epimerite a globular sessile papilla. Spores curved.
- Type: *Amphoroides polydesmi* (Léger) Labbé.
- Genus 21. *Pileocephalus* Schneider 1875:591. Epimerite a lance-shaped cone on a short neck. Spores biconical.
- Type: *Pileocephalus chinensis* Schn.
- Genus 22. *Stylocystis* Léger 1899:526. Epimerite a sharply recurved cone. Spores biconical.
- Type: *Stylocystis praecox* Léger.
- Genus 23. *Discorhynchus* Labbé 1899:20. Epimerite a large globular papilla with a thin collar at the base, neck short. Spores biconical, slightly curved.
- Type: *Discorhynchus truncatus* (Léger) Labbé.
- Genus 24. *Steinina* Léger and Duboscq 1904:352. Epimerite a short mobile digitiform process changing into a flattened disc. Spores biconical.
- Type: *Steinina ovalis* (Stein) L & D.
- Genus 25. *Anthorhynchus* Labbé 1899:19. Epimerite a large fluted flattened disc. Spores biconical, extruded in chains laterally.
- Type: *Anthorhynchus sophiae* (Schn.) Labbé.
- Genus 26. *Sciadophora* Labbé 1899:18. Epimerite a large sessile disc with crenulate periphery. Protomerite with numerous backwardly-directed vertical laminations. Spores biconical.
- Type: *Sciadophora phalangii* (Léger) Labbé.
- Genus 27. *Amphorocephalus* Ellis 1913:462. Epimerite a sessile peripherally fluted disc set upon a short dilated neck. Protomerite constricted superficially across middle. (Spores unknown.)
- Type: *Amphorocephalus amphorellus* Ellis.
- Genus 28. *Pyxinia* Hammerschmidt 1838:357. Epimerite a flat crenulate crateriform disc from the center of which rises a long or short style. Spores biconical.
- Type: *Pyxinia rubecula* Hamm.
- Genus 29. *Schneideria* Léger 1892:153. Epimerite sessile, a thick horizontal disc with milled border, from center of which projects up a short style. No protomerite in adults. Spores biconical.

- Type: *Schneideria mucronata* Léger.
- Genus 30. *Asterophora* Léger 1892:129. Epimerite like *Schneideria*, with longer style. Spores cylindro-biconical.
- Type: *Asterophora mucronata* Léger.
- Genus 31. *Beloïdes* Labbé 1899:27. Epimerite a short stout neck with spiny globule at apex. Spores biconical.
- Type: *Beloïdes firmus* (Léger) Labbé.
- Genus 32. *Actinocephalus* Stein 1848:196. Epimerite sessile or with short neck, at apex of which are eight to ten short sharp or simple digitiform processes. Spores biconical.
- Type: *Actinocephalus conicus* (Duf.) Frantz.
- Genus 33. *Taeniocystis* Léger 1906:307. Epimerite small sessile sphere set with six or eight recurved hooks. Deutomerite divided by septa into many linear segments. Spores biconical.
- Type: *Taeniocystis mira* Léger.
- Genus 34. *Stictospora* Léger 1893:129. Epimerite with a short neck, a spherical crateriform ball with twelve backwardly-directed laminations set close to neck. Spores biconical, slightly curved.
- Type: *Stictospora provincialis* Léger.
- Genus 35. *Bothriopsis* Schneider 1875:596. Epimerite sessile, small, ovoidal, set with six or more long slender filaments directed upward. Spores biconical. Protomerite wider than deutomerite, septum convex upward.
- Type: *Bothriopsis histrio* Schn.
- Genus 36. *Coleorhynchus* Labbé 1899:23. Protomerite a shallow disc with scalloped cape down over upper part of deutomerite. Spores biconical.
- Type: *Coleorhynchus heros* (Schn.) Labbé.
- Genus 37. *Legeria* Labbé 1899:24. Protomerite broader than deutomerite, septum convex upward; spores cylindro-biconical. (Epimerite unknown.)
- Type: *Legeria agilis* (Schn.) Labbé.
- Genus 38. *Geneiorhynchus* Schneider 1875:594. Epimerite a tuft of short bristles at apex of a long slender neck, spores cylindro-biconical.
- Type: *Geneiorhynchus monnieri* Schn.
- Genus 39. *Hoplorhynchus* Carus 1863:570. Epimerite a flat disc with eight to ten short digitiform processes at apex of a long neck. Spores biconical.
- Type: *Hoplorhynchus oligacanthus* (von Sieb.) Schn.
- Genus 40. *Phialoides* Labbé 1899:24. Epimerite a cushion set peripherally with stout teeth around the base a collar larger than the cushion, upon a long slender neck. Spores biconical.
- Type: *Phialoides ornata* (Léger) Labbé.
- Family 8. *Acanthosporidae* Léger 1892:167. Sporonts solitary, epimerites complex. Cyst dehiscence by simple rupture. Spores with equatorial and polar spines.

Genus 41. *Acanthospora* Léger 1892:145. Epimerite a simple conical knob. Spores biconical with a row of equatorial and one of polar spines.

Type: *Acanthospora pileata* Léger.

Genus 42. *Corycella* Léger 1892:144. Epimerite globular, with eight large recurved hooks. Spores biconical with one row of polar spines.

Type: *Corycella armata* Léger.

Genus 43. *Prismatospora* Ellis 1914:215. Epimerite subglobular with eight lateral recurved hooks. One row of spines at each pole. Spores hexagonal.

Type: *Prismatospora evansi* Ellis.

Genus 44. *Ancyrophora* Léger 1892:146. Epimerite globular with five to ten backwardly-directed digitiform processes. Spores biconical with one row of equatorial and one of polar spines.

Type: *Ancyrophora gracilis* Léger.

Genus 45. *Cometoides* Labbé 1899:29. Epimerite a globe with six to eight long slender filaments directed upward. Spores cylindro-biconical with one row of polar and two of equatorial spines.

Type: *Cometoides crinitus* (Léger) Labbé.

Family 9. Menosporidae Léger 1892:168. Sporonts solitary. Epimerite a large cup bordered with hooks and placed on a long slender neck. Cyst dehiscence by simple rupture. Spores crescentic, smooth.

Genus 46. *Menospora* Léger 1892:151, 168. Characters of the family.

Type: *Menospora polyacantha* Léger.

Family 10. Stylocephalidae Ellis 1912:25. Sporonts solitary, epimerites varied. Nucleus ovoidal. Dehiscence by pseudocyst. Spores hat-shaped, in chains.

Genus 47. *Stylocephalus* Ellis 1912:25. Dilated papilla at end of a long neck. Spores hat-shaped. Cysts covered with minute papillae.

Type: *Stylocephalus oblongatus* (Hamm.) Wats.

Genus 48. *Bulbocephalus* Watson 1916b:66. Epimerite a dilated papilla in middle of a long slender neck.

Type: *Bulbocephalus wardi* Wats.

Genus 49. *Sphaerorhynchus* Labbé 1899:32. Epimerite a small sphere at the end of a long slender neck.

Type: *Sphaerocystis ophioides* (Schn.) Labbé.

Genus 50. *Cystocephalus* Schneider 1886:99. Epimerite a large lance-shaped papilla at end of a short neck. Spores hat-shaped.

Type: *Cystocephalus algerianus* Schn.

Genus 51. *Oocephalus* Schneider 1886:101. Epimerite a sphere at apex of a short stout neck.

Type: *Oocephalus hispanus* Schn.

Genus 52. *Lophocephalus* Labbé 1899:31. Sessile crateriform disc with crenulate periphery, set at the base with many short upwardly-directed digits.

Type: *Lophocephalus insignis* (Schn.) Labbé.

Family 11. Dactylophoridae Léger 1892:165. Sporonts solitary, epimerites highly complex, asymmetric, digitate. Cyst dehiscence by pseudocyst, spores elongate-cylindrical. Parasites in Chilopods.

Genus 53. *Echinomera* Labbé 1899:16. Epimerite an eccentric cone with eight or more short upwardly-directed digitiform processes, persistent. Cyst dehiscence by simple rupture, spores cylindrical, extruded in chains.

Type: *Echinomera hispida* (Schn.) Labbé.

Genus 54. *Rhopalonia* Léger 1893:1285. Epimerite a subspherical cushion with ten or more short thick outwardly directed digits. Pseudocyst. Spores cylindrical.

Type: *Rhopalonia geophili* Léger.

Genus 55. *Trichorhynchus* Schneider 1882:438. Protomerite with long slender neck dilated at end in an eccentric cone. Cyst-dehiscence by pseudocyst, spores cylindrical to ellipsoidal.

Type: *Trichorhynchus pulcher* Schn.

Genus 56. *Seticephalus* Kamm 1922. Epimerite a dense tuft of short upwardly-directed brush-like bristles on top of the broad flat protomerite.

Type: *Seticephalus elegans* (Pinto) Kamm.

Genus 57. *Dactylophorus* Balbiani 1889:41. Protomerite dilated laterally at the top and set with peripheral digitiform processes. Cyst dehiscence by pseudocyst, spores cylindrical.

Type: *Dactylophorus robustus* Leger.

Genus 58. *Nina* Grebnecki 1873: ? Protomerite two long lobes fused at one end, set peripherally with teeth and long filaments. Cyst dehiscence by pseudocyst. Spores long-ovoidal, in chains obliquely.

Type: *Nina gracilis* Grebnecki.

Genus 59. *Acutispora* Crawley 1903:632. Epimerite not described. Spores long, ellipsoidal with a lengthwise-directed rod at each end. Cyst dehiscence by pseudocyst.

Type: *Acutispora macrocephala* Crawl.

GENERA OF UNCERTAIN POSITION

Genus 60. *Metamera* Duke 1910:261. Epimerite an eccentric cone set peripherally with numerous branched digitiform processes. Cyst dehiscence by simple rupture. Spores obese biconical.

Type: *Metamera schubergi* Duke.

Genus 61. *Agrippina* Strickland 1912:108. Sporonts solitary, epimerite a circular disc armed with peripheral digitiform processes, on a short neck. Spores long ovoidal.

Type: *Agrippina bona* Strick.

Genus 62. *Ganymedes* Huxley 1910:155. Sporonts associative. A motile stalked sphere at anterior end, cup at posterior end. No septum, no true epimerite. Cysts spherical. Alimentary tract of Crustacea.

Type: *Ganymedes anaspidis* Hux.

Genus 63. *Nematoides* Mingazzini 1891:233. Dicystid, no septum in sporonts. Epimerite forked, at apex of a long neck.

Type: *Nematoides fusiformis* Ming.

A GROUP OF TABLES SHOWING THE PHYLOGENETIC RELATIONSHIPS OF GREGARINES

Table 1. Showing the Intermediate Position of Two Families, LECUDINIDAE AND POLYRHABDINIDAE

	Septum	Epimerite, character	Spores	Host	Habitat
Tribe Acephalina	Absent	Absent	Biconical or with dissimilar poles	Echinoderms, marine and terrestrial Annelids, a few Arthropods	Generally coelomic
Family Lecudinidae	Absent	Present, simple	Dissimilar poles	Marine Annelida	Digestive tract
Family Polyrrhabdinidae	Present	Present, varied	?	Marine Annelida	Digestive tract
Tribe Cephalina	Present	Present, varied	All poles alike	Arthropoda	Digestive tract

Table 2. Showing Relationships of the Families of the Tribe Cephalina

Family	Sporont	Epimerite	Development	Cyst dehiscence	Spores	Host	Remarks
1. Lecudinidae } 2. Polyrrhabdinidae }	See Table I						
3. Cephaloidophoridae	Twos	Absent	Intracellular	Simple rupture	Ovoidal with equatorial line	Crustacea	
4. Stenophoridae	Solitary	Absent or rudimentary	Intracellular	Simple rupture	Ovoidal with equatorial line	Diplopods	
5. Gregarinidae	Solitary or in associations up to 12	Simple, symmetrical	Extra-cellular	Spore-ducts or simple rupture	Ellipsoidal	Insects chiefly	
6. Didymophyiidae	Associations of 2 or 3	Small, simple papilla	"	Simple rupture	Ellipsoidal	Crustacea and Coleoptera	No septum in satellites
7. Actinocephalidae	Solitary	Complex	"	Simple rupture	Irregular or biconical or cylindrical-biconical	Insects and Chilopods	
8. Acanthosporidae	Solitary	Complex	"	Simple rupture	With equatorial and polar spines	Insects	
9. Menosporidae	Solitary	Long neck, cup with spines at top	"	Simple rupture	Crescentic	Insects	
10. Stylocephalidae	Solitary	Long neck (except one genus) with simple apex	"	Pseudocyst	Irregular brown or black	Insects	
11. Dactylophoridae	Solitary	Highly complex asymmetric digitate	"	Pseudocyst	Elongate-cylindrical	Chilopods	

Table 3. Showing Relationships Between Genera in the Family Gregarinidae

Genus	Sporont	Epimerite	Cyst dehiscence	Spores	Remarks
1. Leidyana	Solitary	Sessile globe	Spore-ducts	Barrel-shaped, in chains	
2. Gregarina	In twos	Simple globular or cylindrical papilla	Spore-ducts	Barrel-shaped, in chains	
3. Protomagalhaensia	Several	?	?	Barrel-shaped, with spine at each corner	Sporonts attenuate, attachment often lateral
4. Gamocystis	In twos	?	Spore-ducts, sporulation partial	Cylindrical	Protomerite only in trophic stages
5. Hyalospora	In twos	Simple globular knob	Simple rupture	Ellipsoidal	Endoplasm yellow-orange
6. Hirmocystis	Two to 12	Small cylindrical papilla	Simple rupture	Ovoidal	
7. Euspora	In twos	?	Simple rupture	Prismatic	
8. Sphaerocystis	Solitary	?	Simple rupture	Ovoidal	Protomerite only in trophic stages
9. Cnemidospora	Solitary	?	Simple rupture	Ellipsoidal	Protomerite one-half gray, other yellow-green
10. Uradiophora	In twos	Elongate papilla	Simple rupture	Spherical or subspherical, in chains	Deutomerite with small appendix, Crustacea
11. Pyxinoides	In twos	Slightly stalked globular papilla with 16 longitudinal furrows and a small cone at apex		?	Crustacea

Table 4. Showing Relationships Between Genera in the Family Actinocephalidae

Genus	Epimerite	Spores	Remarks
1. Amphoroides	Sessile globular papilla	Curved biconical	
2. Pileocephalus	Short dilated neck, lance-shaped cone at apex	Biconical	
3. Stylocystis	Recurved sharply pointed cone	Biconical	
4. Discorhynchus	Short neck, large globe with thin collar around base	Biconical, slightly curved	
5. Steinina	A short mobile digitiform process changing into a flat crenulate disc	Biconical	
6. Anthorhynchus	Sessile large fluted flattened disc	Biconical	Extruded in chains, laterally
7. Sciadophora	A large sessile peripherally crenulate disc	Biconical	Protomerite with numerous backwardly-directed vertical laminations
8. Amphorocephalus	Concave peripherally crenulate fluted disc set upon a short dilated neck	?	

Table 4. (Continued)

Genus	Epimerite	Spores	Remarks
9. Pyxinia	Flat crenulate crateriform disc from center of which rises a long or short style	Biconical	
10. Schneideria	Sessile, a thick horizontal disc with milled border, short style projecting up from center	Biconical	No protomerite in adults; a degenerate rather than rudimentary character
11. Asterophora	Like last, with central style longer	Cylindro-biconical	
12. Beloides	Short stout neck with spiny globe at apex	Biconical	
13. Actinocephalus	Sessile or with short neck, at apex 8 to 10 short sharp spines or simple processes	Biconical	
14. Taeniocystis	Small sessile sphere set with 6 or 8 recurved hooks	Biconical	Deutomerite divided by septa into many linear segments
15. Stictospora	Short neck, spherical crateriform ball with 12 backwardly-directed laminate filaments set close to neck	Biconical, slightly curved	
16. Bothriopsis	Sessile, very small, ovoidal, with 6 or more long slender filaments directed upward	Biconical	Protomerite wider than deutomerite, septum convex upward
17. Coleorhynchus	?	Biconical	Septum convex upward. Prot. a shallow disc with scalloped cape over deutomerite
18. Legeria	?	Cylindro-biconical	Protomerite broader than deutomerite, septum convex upward
19. Geneiorhynchus	Long slender neck, tuft of short bristles at apex	Cylindro-biconical	
20. Hoplorhynchus	Long neck, flat disc with 8 to 10 digitiform processes at apex	Biconical	
21. Phialoides	Long slender neck, at apex a broad cushion with peripheral teeth surrounded at base with a collar larger than the cushion	Biconical	

The epimerites of this family are surprisingly well correlated. The genera with short necks form a regular succession; the simple globe (1) becomes slightly modified (2), (3); then a disc develops at the base (4), (5), (6), (7), (8); with a style rising in the center (9), (10). This seems to be the end of one line of development.

The simple sessile or nearly sessile globule becomes spiny (12), (13); the spines become simple digitiform processes or recurved hooks (14); the recurved hooks become attached to the neck along their whole length (15). The processes change into long slender filaments (16)—and probably (17) and (18). The neck becomes long and slender, and at the apex there develops a tuft of short bristles (19), a flat disc with 8 to 10 peripheral digits (20), or stout teeth (21).

Table 5. Showing the Relationships Between the Genera in the Family Acanthosporidae

Genus	Epimerite	Spores
1. Acanthospora	Simple conical knob	Biconical, row of equatorial and one of polar spines
2. Corycella	Globular, with 8 large recurved hooks	Biconical, one row of polar spines
3. Prismatospora	Subglobular, with 8 lateral recurved hooks	One row of spines at each pole. Hexagonal
4. Ancyrophora	Globular, with 5 to 10 backwardly directed digitiform processes	Biconical, with one row of equatorial and one of polar spines.
5. Cometoides	Globe, with 6 to 8 long slender filaments directed upward	Cylindro-biconical, with one row of polar and two of equatorial spines

Table 6. Showing Relationships Between the Genera in the Family Stylocephalidae

Genus	Epimerite	Spores	Remarks
1. Stylocephalus	Long neck, dilated papilla at apex	Hat-shaped	Cysts covered with small papillae
2. Bulbocephalus	Long neck, dilated papilla midway	?	
3. Sphaerorhynchus	Long neck, small sphere at apex	?	
4. Cystocephalus	Short stout neck, large lance-shaped papilla at apex	Hat-shaped	
5. Oocephalus	Short neck with sphere at apex	?	
6. Lophocephalus	Sessile crateriform disc with crenulate periphery, set at base with many short upwardly-directed digits	Hat-shaped	

I can see very little relationship between the genera of this family as a whole. (1), (2), and (3) are related, as are (4) and (5), but the three groups seem to bear no epimeritic relationship whatever. The hat-shaped spores, however, connect the seemingly aberrant genus (6), with the type.

Table 7. Showing Relationships Between the Genera in the Family Dactylophoridae

Genus	Character of protomerite or epimerite	Cyst dehiscence	Spores	Remarks
1. Echinomera	Epimerite an eccentric cone with eight or more short upwardly-directed digitiform processes, persistent	Simple rupture	Cylindrical in chains	
2. Rhopalonia	Epimerite a subspherical cushion with ten or more short thick outwardly-directed digits	Pseudocyst	Cylindrical	No protomerite in adult
3. Trichorhynchus	Protomerite with long slender neck dilated at end in an eccentric cone	Pseudocyst	Cylindrical to ellipsoidal	
4. Seticephalus	A dense tuft of short upwardly-directed brush-like bristles on top of a broad flat protomerite	?	?	
5. Dactylophorus	Protomerite dilated laterally with peripheral digitiform processes	Pseudocyst	Cylindrical	
6. Nina	Protomerite two long lobes fused at one end, set peripherally with teeth and long filaments	?	Long-ovoidal	Spores in chains obliquely
7. Acutispora	?	Pseudocyst	Long-ellipsoidal with a lengthwise-directed rod at each end	

SYNOPSIS OF THE GREGARINES FROM VARIOUS GROUPS OF
THE ANIMAL KINGDOM

LIST OF SPECIES FOUND IN THE PHYLUM COELHELMINTHES*

PARASITE	Host
LECUDINIDAE	
<i>Lecudina pellucida</i> (Kölliker) Mingazzini	<i>Nereis cultrifera</i>
Type species	<i>N. beaucourdrayi</i> Aud.
<i>Lecudina leuckarti</i> Mingazzini	<i>Sagitta</i> sp.
<i>Lecudina aphroditae</i> (Lankester) Kamm	<i>Aphrodite aculeata</i>
<i>Lecudina elongata</i> (Mingazzini) Kamm	<i>Lumbriconereis impatiens</i> Clap.
<i>Lecudina heterocephala</i> (Mingazzini) Kamm	<i>Nephtys scolopendroides</i> delle Chiaje
<i>Lecudina polydorae</i> (Léger) Kamm	<i>Polydora agassizi</i> Clap.
	<i>P. ciliata</i>
<i>Lecudina</i> sp. Saint-Joseph	<i>Polymnia nebulosa</i> M.
	<i>Notomastus exsertilis</i> N. S.
	<i>Petaloproctus terricola</i> Qfg.
<i>Lecudina legeri</i> (Brasil) Kamm	<i>Glycera convoluta</i> Kef.
<i>Lecudina</i> sp. Faria, Cunha, and Fonseca	<i>Polydora socialis</i> Schm.
POLYRHABDINIDAE	
<i>Polyrhabdina spionis</i> (Kölliker) Mingazzini	<i>Scololepsis fuliginosa</i>
Type species	<i>S. ciliata</i>
<i>Polyrhabdina brasili</i> Caullery and Mesnil	<i>Spio martinensis</i>
<i>Polyrhabdina pygospionis</i> Caullery and Mesnil	<i>Pygospionis seticornis</i>
<i>Sycia inopinata</i> Léger	<i>Audouinia Lamarckii</i>
Type species	
<i>Ulivina elliptica</i> Mingazzini	<i>Audouinia filigera</i> (d. Chiaje)
Type species	<i>A. tentaculata</i> Mont.
	<i>Petaloproctus terricola</i> Qfg.
	<i>Nicolea venustula</i> Mont.
	<i>Polymnia nebulosa</i> Mont.
<i>Ulivina rhynchoboli</i> (Crawley) Kamm	<i>Rhynchobolus americanus</i> Ver.
GENUS OF UNCERTAIN POSITION	
<i>Metamera schubergi</i> Duke	<i>Glossosiphonia complanata</i>
Type species	<i>Hemiclepsis marginata</i>
<i>Metamera</i> sp. Ellis	<i>Clepsine elongata</i>
SPECIES OF UNCERTAIN POSITION	
? <i>Taeniocystis legeri</i> Cognetti de Martiis	<i>Kynotus Pittarelli</i>

Family LECUDINIDAE Kamm (nov. fam.)

Epimerite symmetrical, simple. Body non-septate. Spores ovoidal, asymmetrical, thickened at one pole. Intestine of marine annelids.

*The parasites are arranged in chronological order under each genus in this and all similar succeeding lists.

DISCUSSION OF THE NEW FAMILY LECUDINIDAE

The type genus of this family, *Lecudina* was named by Mingazzini in 1891. Two years later Léger, working independently, designated a new genus *Doliocystis* for the species described by Mingazzini. The earlier work has been overlooked by subsequent workers while the name used by Léger has come into frequent usage, the genus being raised to family rank (*Doliocystidae*) by Labbé, in 1899.

In Table I of Chapter II, is shown the intermediate position of the family *Lecudinidae* and the somewhat related family, the *Polyrhabdinidae*. The *Lecudinidae* are related to the Tribe *Acephalina*, for they are non-septate, there being but one division in the body at all stages of development.

All the members of the Tribe *Cephalina*, on the other hand, are characterized by the presence of a septum, which divides the body into a protomerite and deutomerite, if not in the adult, at least in the trophic stages of development. When the septum is absent from the adult, it is clearly a degenerative rather than a rudimentary character, all other generic features conforming to the type.

(Cf. *Schneideria*, *Sphaerocystis*, *Rhopalonia*, *Gamocystis*.)

The *Lecudinidae*, however, possess only the epimeritic demarkation from the rest of the body, and when this structure disappears, the body is unilocular. Léger (1893) remarks:

. . . la grégarine présente toujours deux segments: le segment intra-cellulaire ou *épimérite*, et le segment extra-cellulaire dans lequel s'est porté le noyau. C'est donc seulement à ce moment que la grégarine se montre comme une véritable dicystidée. . . les jeunes individus abandonnent leur *épimérite* et deviennent libres dans l'intestin, présentant à lors toutes les apparences de véritable *Monocystis*

In the type species, *Lecudina pellucida* (Köll.) Ming., there is a differentiation in the protoplasm of the anterior end (what would be the protomerite in polycystids) from that of the remainder of the body. This was illustrated by Kölliker (my fig. 126) but not mentioned by Léger in 1893. Brasil (1909) illustrates this differentiation clearly in both trophozoite and sporont (my figs. 134 and 135).

If normally present, and I have no doubt that it is but often not mentioned or discovered, this character is an important one in assigning the family in question to an intermediate position between the monocystids and the polycystids.

In its cyst-formation and spore type, the family follows the polycystid type.

After the above had been written, this statement from Minchin (1903) was found:

The possession of an epimerite is a feature is used for classifying which the Gregarines, and the legion *Eugregarinae* is separated into the two sub-orders *Cephalina* and *Acephalina*, according to the presence or absence of this appendage. As a general rule the forms which

possess an epimerite have the body behind it divided into protomerite and deutomerite by a septum, and have hence been termed Polycystida . . . , while those without an epimerite are also without a septum; hence Monocystida But in one family, Doliocystidae, Labbé, an epimerite is present, and may attain a considerable size . . . without any septum dividing the rest of the body It is purely a matter of definition whether those forms be considered as Cephalina without a septum, or as Monocystis with an epimerite. The Cephalina in which the body is non-septate are sometimes distinguished as Dicystida from those in which there is a distinct protomerite and deutomerite (Tricystida). These terms are to be understood, however, in a purely descriptive sense, and cannot be used for classificatory purposes, as there is no doubt that many dicystid species are derived from tricystid forms secondarily, by obliteration of the protomerite On the other hand, such forms as the Doliocystidae appear to be truly and primitively dicystid, and are to be regarded as intermediate forms transitional from Acephalina to Cephalina.

Genus LECUDINA MINGAZZINI 1891: 469

Body non-septate, epimerite regularly simple. Spores ovoidal, thickened at one pole.

LECUDINA PELLUCIDA (Kölliker) Mingazzini Type species

[Figure 126]

1848	<i>Gregarina pellucida</i>	Kölliker	1848: 35
1851	<i>Gregarina pellucida</i>	Diesing	1851: 17
1859	<i>Gregarina pellucida</i>	Diesing	1859: 739
1872	<i>Monocystis nereidis</i>	Lankester	1872: 343
1891	<i>Lecudina pellucida</i>	Mingazzini	1891: 469
1893	<i>Lecudina pellucida</i>	Mingazzini	1893: 51
1893	<i>Doliocystis pellucida</i>	Léger	1893: 204
1899	<i>Doliocystis pellucida</i>	Labbé	1899: 33
1903	<i>Doliocystis pellucida</i>	Minchin	1903: 202, 327
1909	<i>Doliocystis pellucida</i>	Brasil	1909: 119
1913	<i>Doliocystis pellucida</i>	Ellis	1913: 287

Sporonts solitary, ellipsoidal or "bottle-shaped," rectangular or rounded at anterior end and broadly rounded at posterior. Nucleus spherical. Epimerite a simple small papilla.

Cysts small, dehiscence by simple rupture, spores ovoidal, 7 by 5 μ , with thickening at one pole.

Taken at Triest, Naples, and in the Gulf of Marseilles.

Intestine of *Nereis cultrifera* Grube and *N. beaucourdrayi* Aud. Kölliker's figure indicates a differentiation in the protoplasm of the anterior end of the body from that of the remainder.

Mingazzini describes the body as nearly transparent, especially at the anterior end, and both mentions and illustrates the retractility of the anterior end within the body.

LECUDINA LEUCKARTI Mingazzini

1860	No name	Leuckart	1860: 263
1891	<i>Lecudina Leuckarti</i>	Mingazzini	1891: 469
1893	<i>Lecudina Leuckarti</i>	Mingazzini	1893: 51

Similar to the type species, the anterior end not constricted bottle-like.
Intestine of *Sagitta* sp.

LECUDINA APHRODITAE (Lankester) Kamm

[Figure 125]

1863	<i>Monocystis aphroditae</i>	Lankester	1863: 90, 94
1871	Unnamed	Stuart	1871: 498
1899	<i>Doliocystis aphroditae</i>	Labbé	1899: 33
1903	<i>Doliocystis aphroditae</i>	Minchin	1903: 176, 202, 326
1909	<i>Doliocystis aphroditae</i>	Brasil	1909: 120
1922	<i>Lecudina aphroditae</i>	Kamm	1922 (this paper)

One-half inch in length. "This is the only unilocular form of Gregarina which at present has been found provided with a proboscis."
Lankester.

Intestine of *Aphrodite aculeata*.

LECUDINA ELONGATA (Mingazzini) Kamm

[Figures 134 and 135]

1891	<i>Ophiodina elongata</i>	Mingazzini	1891: 471
1893 ⁴⁷	<i>Ophiodina elongata</i>	Mingazzini	1893: 53
1899	<i>Doliocystis elongata</i>	Labbé	1899: 33
1903	<i>Doliocystis elongata</i>	Minchin	1903: 327
1908	<i>Doliocystis elongata</i>	Brasil	1908: 355
1908	<i>Doliocystis elongata</i>	Brasil	1908a: 425
1909	<i>Doliocystis elongata</i>	Brasil	1909: 112
1922	<i>Lecudina elongata</i>	Kamm	1922 (this paper)

Sporonts solitary, elongate-cylindrical, attaining 500 μ by 40 μ . Protoplast of anterior end highly specialized from that of remainder. Nucleus large, spherical, with several karyosomes.

An intracellular stage was encountered by Brasil, who thinks it may be schizogonic in character. It is possible, however, that it may have been a portion of the life-history of another parasite.

Mingazzini describes the epimerite as a "piccolo bottone sferico"; Brasil finds a long thread-like filament which penetrates to the base of the cell, which is certainly atypical.

Intestine of *Lumbriconercis impatiens* Claparede.

Taken at Naples.

In three of Mingazzini's twelve illustrations of the species, there is some indication of a septum present, the protoplasm being quite different in the two portions.

I can see no differentiation between the two genera described by Mingazzini, *Lecudina* and *Ophiodina*, from the meagre data known concerning each. The intracellular development and the spores may reveal differences, however. From the existing data, I have united the two under the name of the first-named genus, *Lecudina*.

LECUDINA HETEROCEPHALA (Mingazzini) Kamm

1891	<i>Ophiodina heterocephala</i>	Mingazzini	1891: 473
1893	<i>Ophiodina heterocephala</i>	Mingazzini	1893: 54
1899	<i>Doliocystis heterocephala</i>	Labbé	1899: 34
1903	<i>Doliocystis heterocephala</i>	Minchin	1903: 327
1922	<i>Lecudina heterocephala</i>	Kamm	1922 (this paper)

Sporonts very elongate, vermiform. Epimerite "a sort of papilla" at anterior end. Protoplasm of anterior end differentiated from that of body proper.

Nucleus spherical, with one or two karyosomes.

Intestine of *Nephthys scolopendroides* delle Chiaje.

LECUDINA POLYDORAE (Léger) Kamm

1893	<i>Doliocystis polydorae</i>	Léger	1893: 205
1899	<i>Doliocystis polydorae</i>	Labbé	1899: 33
1903	<i>Doliocystis polydorae</i>	Minchin	1903: 327
1909	<i>Doliocystis polydorae</i>	Brasil	1909: 119
1914	<i>Polyrhabdina polydorae</i>	Caullery and Mesnil	1914: 520
1922	<i>Lecudina polydorae</i>	Kamm	1922 (this paper)

Epimerite similar to that described for the type species, but larger. "Epimerite a la forme d'un tronc de cone a petite base inferieure et il se continue directement avec l'extremite anterieure du second segment, allongee en forme de col." Léger.

Intestine of *Polydora agassizi* Clap.; *P. ciliata*.

Taken in the Gulf of Marseilles, France.

LECUDINA sp. Saint-Joseph

1907	<i>Doliocystis</i> sp.	Saint-Joseph	1907: 145, 172, 173
1911	<i>Doliocystis</i> sp.	Sokolow	1911: 287
1922	<i>Lecudina</i> sp.	Kamm	1922 (this paper)

Measurements are given of sporonts from various polychaetes, as follows: 84μ by 29μ ; 470μ by 63μ ; 300μ by 48μ . It is quite possible that several species are involved, but no description is given of any one.

Intestine of *Polymnia nebulosa* M.; *Notomastus exsertilis* N.S.; and *Petaloproctus terricola* Qfg.

LECUDINA LEGERI (Brasil) Kamm

1909	<i>Doliocystis legeri</i>	Brasil	1909: 71, 123
1911	<i>Doliocystis legeri</i>	Sokolow	1911: 284
1922	<i>Lecudina legeri</i>	Kamm	1922 (this paper)

Sporonts cylindrical, 100μ by 25μ . Nucleus ovoidal, with one karyosome. Epimerite a rhizoid filament which penetrates to the base of the host-cell (Brasil).

Cysts small, 45μ in diameter, spores typical, releasing eight sporozoites.

Intestine of *Glycera convoluta* Kef.

Taken on the Mediterranean Coast.

LECUDINA sp. Faria, Cunha, and Fonseca

1918	<i>Doliocystis</i> sp.	Faria, Cunha, and Fonseca	1918: 17
1922	<i>Lecudina</i> sp.	Kamm	1922 (this paper)

Sporonts spindle-shaped, nucleus spherical.

Host: *Polydora socialis* Schmerda.

Taken near Rio de Janeiro, Brazil.

Not enough data exists to definitely fix the position of this species.

Family POLYRHABDINIDAE Kamm 1922 (this paper)

Polycystid (septate) gregarines inhabiting the digestive tract of polychaetes. Epimerites varied.

DISCUSSION OF THE NEW FAMILY POLYRHABDINIDAE

The true septate intestinal gregarines of marine annelids fall under three genera, which are placed in various positions by different workers on the subject:

(a) Two genera were described very meagerly by Mingazzini in 1891 under one name, *Polyrhabdina*, two very different parasites being found in the same host material. The one has been removed to the *Schizogregarines* (*Selenidium*), while the other represents the genus as named, and is a pyriform septate species which possesses an epimerite in the shape of a corona of hooks.¹

(b) The genus *Sycia* Léger 1892 is characterized by its septate sporonts and unique epimerite in the form of a large rounded papilla with a thick

¹ Mingazzini's description follows: . . . specie dimorfe. Individue a forme di nematode e piriformi. I primi hauno il corpo allungato fusiforme e la cuticula striata longitudinalmente du rialzi numerosi finissimi.

ring or collar around the base. The deutomerite of the adult sporont, only, contains numerous elongate crescentic or ellipsoidal inclusions probably "reserve protoplasm."

(c) The third genus, *Ulivina* Mingazzini 1891, has little to characterize it. In fact so little is known concerning its development that it cannot be placed with either of the two named genera and hence must stand distinct until its position shall have been proven. The epimerite, is simple so far as known and cyst and spores are unknown.

The cysts and spores are still unknown for all three genera.

Since a septum is present without exception in all three, they must be included in the suborder Cephalina, but stand near the borderline with the Acephalina because of their presence only in polychaetes.

Genus POLYRHABDINA Mingazzini 1891:229

(*Polyrhabdina* Labbé 1899:48)

Septate, sporonts flattened, ovoidal, epimerite a corona of hooks. Intestine of polychaetes of the family Spionidae. (Cyst and spores unknown.)

POLYRHABDINA SPIONIS (Kölliker) Mingazzini Type Species

[Figures 128, 129]

1848	<i>Gregarina Spionis</i>	Kölliker	1848: 4
1851	<i>Gregarina Spionis</i>	Diesing	1851: 18
1891	<i>Polyrhabdina Spionis</i>	Mingazzini	1891: 229
1893	<i>Polyrhabdina Spionis</i>	Mingazzini	1893: 56
1903	<i>Doliocystis</i> sp.	Minchin	1903: 327
1914	<i>Polyrhabdina spionis</i>	Caullery and Mesnil	1914: 516

Septum present. Sporonts 100 by 35 μ , ellipsoidal, nucleus spherical, one large karyosome.

Epimerite a flattened apical corona of 8 to 10 ameoboid digitiform processes frequently bifurcate.

Development extracellular. Cyst and spores unknown.

Intestine of *Scololepsis fuliginosa*; *S. ciliata* (?).

Taken at Naples.

Minchin mentions a species from the same host, but places it in the genus *Doliocystis*. Since no data is given and the hosts are identical, it is placed here.

POLYRHABDINA BRASILI Caullery and Mesnil

1914	<i>Polyrhabdina brasili</i>	Caullery and Mesnil	1914: 518
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Sporonts ovoidal, 200 μ in length. Epimerite characteristic, but spines shorter than type.

Cyst and spores unknown.

Host: *Spio martinensis*.

POLYRHABDINA PYGOSPIONIS Caullery and Mesnil

1914 *Polyrhabdina pygospionis* Caullery and Mesnil 1914: 520

No description given.

Host: *Pygospionis seticornis*.

Genus SYCIA Léger 1892: 52

Polycystid intestinal parasite of marine annelids. Epimerite knobbed, bordered by a thick ring. Protomerite subspherical, deutomerite conical, with numerous inclosures.

SYCIA INOPINATA Léger Type Species

[Figures 118 and 119]

1892	<i>Sycia inopinata</i>	Léger	1892: 52, 90
1899	<i>Sycia inopinata</i>	Labbé	1899: 34
1903	<i>Sycia inopinata</i>	Minchin	1903: 203, 326
1909	<i>Sycia inopinata</i>	Brasil	1909: 121

Septate gregarine, ellipsoidal. No dimensions given. Ratio LP : TL :: 1:6; WP : WD :: 1:1.5. Protomerite conoidal, broadest at septum. Deutomerite ellipsoidal, tapering rapidly to a sharp point. Nucleus large, spherical, one karyosome.

Epimerite an elongate papilla upon a short neck around which is a collar a little larger than the papilla itself.

Intestine of *Audouinia Lamarkii* (*A. tentaculata*—Brasil).

Taken at Belle-Isle-sur-Mer, France.

Caullery and Mesnil (1914) give the host name as the latter above, and note

. . . c'est une espèce voisine, sinon identique, que Mingazzini (1891) a dénommée *Ulivina* n. g. *elliptica*

but since the cyst and spores of both species are unknown, this cannot at present be determined.

This species possesses characteristic elongate crescentic or biconical inclusions in the deutomerite only of adult sporonts. (Fig. 119). Léger offers the hypothesis that they may be condensations of protoplasm in reserve masses.

Brasil found this species with its epimerite and the inclusions, thus verifying Léger's work of sixteen years previous.

Genus ULIVINA Mingazzini 1891: 235

Body elongate-ellipsoidal, "external membrane continuous around animal." Protomerite the more dense. Epimerite simple, spores unknown. Intestine of marine polychaetes.

ULIVINA ELLIPTICA Mingazzini Type Species

[Figure 127]

1891	<i>Ulivina elliptica</i>	Mingazzini	1891: 235
1899	<i>Ulivina elliptica</i>	Labbé	1899: 34
1903	<i>Ulivina elliptica</i>	Minchin	1903: 203, 326
1907	<i>Ulivina elliptica</i>	Saint-Joseph	1907: 164, 174

Sporonts solitary, ellipsoidal, tapering to a sharply rounded posterior end. Nucleus ovoidal, two or three karyosomes. Dense and opaque. No dimensions given by the original author. Ratio LP:TL::1:4 to 7; WP:WD::1.1:1.

Saint-Joseph mentions dimensions as 150 by 90 μ ; 75 by 33 μ . He illustrates (his fig. 106) a trophozoite with a simple, small, papillate epimerite.

Taken at Naples and off the coast of France.

Intestine of *Audouinia filigera* (delle Chiaje); *A. tentaculata* Mont., *Petaloproctus terricola* Qfg., *Nicolea venustula* Mont., and *Polymnia nebulosa* Mont.

ULIVINA RHYNCHOBOLI (Crawley) Kamm

1897	Unnamed	Porter	1897a: 8
1903	<i>Doliocystis rhynchoboli</i>	Crawley	1903: 56
1913	<i>Doliocystis rhynchoboli</i>	Ellis	1913: 287
1922	<i>Ulivina rhynchoboli</i>	Kamm	1922 (this paper)

Sporonts attain 700 μ in length. A distinct septum, with protoplasm in protomerite the more dense. Epimerite a small pointed papilla with a long slender filament at the end. Nucleus small, spherical.

Intestine of *Rhynchobolus americanus* Verrill.

While the epimerite is described for this and for the preceding species, I am not ready to state that it is the type for the genus.

Porter notes a peculiar attachment of the parasite while free in a watch-glass to the glass, being attached by the anterior end of the protomerite with such force that the animal cannot be withdrawn without destroying it.

Genus of Uncertain Position

METAMERA Duke 1910:261

Sporonts solitary, epimerite subconical, apex eccentric with corona of numerous branched digitiform appendages. Cyst dehiscence by simple rupture. Spores biconical.

METAMERA SCHUBERGI Duke Type Species

[Figures 131, 132, and 133]

1910	<i>Metamera schubergi</i>	Duke	1910: 261
1913	<i>Metamera schubergi</i>	Ellis	1913: 285

Sporonts 150 by 45 μ . Deutomerite with one to three septa posterior to the nucleus. Cysts spherical, spores ovoidal 9 by 7 μ .

Epimerite subconical, apex eccentric with corona of numerous branched digitiform processes.

Taken at Heidelberg and Cambridge, Eng.

Intestine of *Glossosiphonia complanata* and *Hemiclepsis marginata*.

I am not ready to assign this species to a position in the family Dactylophoridae, as placed by the author. The method of cyst-dehiscence is different from the type for that family and the spores are not elongate cylindrical. The host is so far removed from the Chilopoda (to which the named family is confined) that I feel certain the species belongs in a group as yet undescribed. When more similar species shall have been described its position can the better be determined.

METAMERA sp. Ellis

1913	<i>Metamera</i> sp.?	Ellis	1913:285, 287
	Host: <i>Clepsine elongata</i> .		

Species of Uncertain Position

TAENIOCYSTIS LEGERI Cognetti de Martiis

[Figure 130]

1911	<i>Taeniocystis legeri</i>	Cognetti de Martiis	1911:247
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Polycystid gregarine, solitary, protomerite and deutomerite segmented by 16 to 19 septa. 700 to 1600 μ in length.

Epimerite, cyst, and spores unknown.

Taken at Moramanga, Madagascar.

Host: *Kynotus Pittarelli* (oligochaete). Coelomic.

The "protomerite" is divided into three segments, which is unique. The parasite is coelomic rather than intestinal, as are all other polycystid gregarines. The epimerite is unknown. For these reasons it is not placed with the type for the genus. The single nucleus seems to place it with the Protozoa; otherwise it might be a haplosporidian.

LIST OF SPECIES FOUND IN THE PHYLUM MOLLUSCA

Species of Uncertain Position

<i>Gregarina pterotracheae</i> (Stuart) Labbé	<i>Pterotrachea</i> sp.
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GREGARINA PTEROTRACHEAE (Stuart) Labbé

[Figure 136]

1871	<i>Zygocystis Pterotracheae</i>	Stuart	1871: 498
1891	<i>Zygocystis Pterotracheae</i>	Mingazzini	1891: 235
1899	<i>Gregarina pterotracheae</i>	Labbé	1899: 37
1903	“ “	Minchin	1903: 338

Contour of body ovoidal, typically that of the genus *Gregarina*, biassocative. Dimensions not given. Ratio LP:TL :: 1:4; WP:WD :: 1:1.5. Protomerite dome-shaped with slight constriction in middle. Deutomerite ovoidal, well-rounded posteriorly. Epicyte unusually thick. Nucleus large, spherical, one to four karyosomes.

Cyst formed of one individual seen, embedded in muscular tissue of host.

Coelom of *Pterotrachea* sp.

Taken at Odessa.

This species is regarded as of uncertain position because it is the first species of the genus *Gregarina* to be found in the body-cavity of a host. It is the only species described from the molluscs, where one would not expect to find a polycystid and biassocative gregarine. This phylum certainly offers splendid research opportunities, if not to substantiate to repudiate the above work.

Stuart describes in detail the motion of the species, and because I believe it is the first good record of the movements of gregarines, it is reproduced here, as follows:

Die Bewegungen des Thieres sind schlängelnder Art, aber neben den Hauptcontractionen, als deren Resultat die Vorwärtsschiebung der Gregarine erscheint, bemerkt man eine Reihe partieller Contractionen, welche die äusseren Contouren des Körpers wellenförmig umändern. Bei diesen Contractionen wird die weiche innere Körnermasse hin und hergeschoben und nimmt die durch die partiellen Gestaltänderungen des contractilen Schlauches gebildeten Innenräume ein. Der Nucleus folgt diesen Bewegungen in beschränktem Masse mit.

LIST OF SPECIES FOUND IN THE CLASS CRUSTACEA OF THE PHYLUM ARTHROPODA

PARASITE	HOST
DIDYMOPHYIDAE	
<i>Didymophyes longissima</i> (von Siebold) Frantzius	<i>Gammarus pulex</i> von Sieb. <i>Orchestia littorea</i>
GREGARINIDAE	
<i>Uradiophora cuenoti</i> (Mercier) Mercier Type species	<i>Atyaephyra Desmaresti</i> Millet
<i>Pyxinoides balani</i> (Kölliker) Trégouboff Type species	<i>Balanus pusillus</i> Ecker <i>B. tintinnabulum</i> L. <i>B. amphitrile</i> Darw. <i>B. eburneus</i> Gould
<i>Pyxinoides cthamali</i> (Léger and Duboscq) Trégouboff	<i>Cthamalus stellatus</i> Ranz.

CEPHALOIDOPHORIDAE

Cephaloidophora conformis (Diesing) Léger
and Duboscq

Cephaloidophora communis Mawrodiadi
Type species

Cephaloidophora fossor (Léger and Duboscq)
Trégouboff

Cephaloidophora ocellata (Léger and Duboscq)
Kamm

Cephaloidophora maculata Léger and Duboscq

Cephaloidophora talitri Mercier

Cephaloidophora olivia (Watson) Kamm

Cephaloidophora nigrofusca (Watson) Kamm

Cephaloidophora delphinia (Watson) Kamm

Cephaloidophora ampelisca (Nowlin and
Smith) Kamm

Pachygraspus marmoratus Fabr.

Balanus improvisus Darw.

B. tintinnabulum communis L.

B. improvisus gryphica Mün.

B. perforans Brug.

B. amphitrite Darw.

B. eburneus Gould

Pinnotheres pisum Penn.

Eupagurus Prideauxi Leach

Gammarus marinus Leach

Talitrus saltator Mont.

Libinia dubia

Uca pugnax, *U. pugilator*

Talorchestia longicornis Say.

Ampelisca spinipes

GENERA OF UNCERTAIN POSITION

Nematoides fusiformis Mingazzini
Type species

Ganymedes anaspidis Huxley
Type species

Balanus perforatus

Pollicipes cornucopia

Anaspides tasmaniae (Thomp.)

UNNAMED SPECIES OF UNCERTAIN POSITION

[? *gammarii* von Siebold]

[sp. Mawrodiadi]

[? *valettei* Nussbaum]

[? *praemorsa* Diesing]

[? *clausii* Frenzel]

[? *nicaeae* Frenzel]

[sp. Minchin]

Gammarus pulex

Balanus amphitrite pallidus Darw.

B. amphitrite Darw.

B. eburneus Gould

Pollicipes polymerus Say

Cancer pagurus

Phronima sp.

Phronimella sp.

Hyale pontica Rathke

Nebalia serrata

Family DIDYMOPHYIDAE Léger 1892:105

Sporonts in associations of two or three. No septa in satellites.

Genus DIDYMOPHYES Stein 1848:186

Characters of family. Epimerite a small pointed papilla, cyst dehiscence by simple rupture, spores ellipsoidal.

DIDYMOPHYES LONGISSIMA (von Siebold) Frantzius

1839	<i>Gregarina longissima</i>	von Siebold	1839: 58
1848	<i>Didymophyes longissima</i>	Frantzius	1848: 196
1848	<i>Gregarina longissima</i>	Kölliker	1848: 34
1851	<i>Gregarina longissima</i>	Diesing	1851: 15
1859	<i>Gregarina longissima</i>	Diesing	1859: 735
1863	<i>Gregarina longissima</i>	Lankester	1863: 95
1886	<i>Gregarina longissima</i>	Plate	1886: 235
1895	<i>Gregarina</i> sp.	Pfeiffer	1895: 60
1899	<i>Didymophyes longissima</i>	Labbé	1899: 8
1903	<i>Didymophyes longissima</i>	Minchin	1903: 330, 331
1911	<i>Gregarina longissima</i>	Wellmer	1911: 119

Sporonts very elongate, cylindrical, vermiform in movements. Ratio LP : TL :: 1 : 30; WP : WD :: 1 : 1. Primita longer than satellite. Dimensions not given (Kölliker). Nucleus small, spherical, one large karyosome.

Intestine of *Gammarus pulex* von Siebold, *Orchestia littorea*.

Taken in Germany.

The species was first described by von Siebold, who also found another species in *Gammarus pulex*, typically like the Cephaloidophoridae in outline but regarded by him as another form of the same species.

Kölliker studied fresh material adding the data that associations exist of two or three elongate slender individuals arranged in single file and of two satellites attached to the posterior end of the primita. Kölliker recognized the possibility of a new species being involved in von Siebold's material and illustrates this as well as the two modifications mentioned in the type species.

The exclusion of the doubted form was also recognized by Diesing (1859).

Lankester (1863) regards all the following as synonyms:

Gregarina longissima Siebold

? *Gr. diffluens* Diesing

Gr. millaria Diesing (Actinocephalus Stein)

Gr. putanea Leuckart

Gr. Gammari Siebold (Didymophyes Stein)

His basis was the identity of the hosts only.

Plate found in the intestine and coelom of *Gammarus pulex* "band-formig" gregarines 255 μ in max. length, three or four attached together and regards them as belonging to the species in question.

Minchin (1903) questions the inclusion of the last named host as authentic.

Léger and Duboscq (1911) have described a new species, *Cephaloidophora maculata*, from *Gammarus marinus* which is identical with the aberrant species referred to above.

Family GREGARINIDAE Labbé 1899:9

Epimerite symmetrical, simple. Sporonts solitary or in association. Cysts with or without spore-ducts, spores symmetrical.

Genus URADIOPHORA Mercier 1912a

Intestinal parasites. Development extracellular. Epimerite an elongate papilla. Cysts without sporeducts. Spores spherical or subspherical, not united in chains, faint equatorial line. End portion of deutomerite of satellite greatly constricted. Associations of two sporonts.

URADIOPHORA CUENOTI (Mercier) Mercier Type Species

[Figure 63]

1911	<i>Cephaloidophora Cuenoti</i>	Mercier	1911: 51
1911	<i>Cephaloidophora Cuenoti</i>	Sokolow	1911: 286
1912	<i>Uradiophora Cuenoti</i>	Mercier	1912a: xli
1912	<i>Uradiophora Cuenoti</i>	Mercier	1912b; 177
1912	<i>Uradiophora Cuenoti</i>	Trégouboff	1912: lvi
1913	<i>Uradiophora Cuenoti</i>	Ellis	1913: 264

Characters of the genus. Syzygies of two sporonts, infrequently of three. Sporonts very elongate, cylindrical. Ratio LP:TL::1:20 (primate) 1:28 (satellite without appendage). WP:WD::1:1.9 to 1:2. Sporonts 700 μ in max. length. Nucleus sub-spherical. Epimerite an elongate papilla, persistent in sporonts. Deutomerite with small atrophied appendix. Nucleus in adults spherical, with one large karyosome; chromidial bodies frequently found in both protomerite and deutomerite. Cysts ovoidal, 38 to 44 μ in diam. Spores 4 μ in diam.

Intestine of *Atyaephyra Desmaresti* Millet.

Taken at Nancy, France.

Genus PYXINOIDES Trégouboff 1912

Intestinal parasites, extracellular in development. Epimerite a short stype dilated in middle to form a globe with sixteen longitudinal grooves, the free upper end of the style being about 2 μ in length. Septum with small disc-shaped horizontal swelling in middle. Sporont ovoidal, nucleus large, one karyosome. Syzygies of two sporonts, the primate always larger. Cyst and spores unknown.

PYXINOIDES BALANI (Kölliker) Trégouboff Type Species

[Figures 65, 82, 88]

1848	<i>Gregarina balani</i>	Kölliker	1848: 35
1848	<i>Stylorhynchus Balani</i>	Frantzius	1848: 195
1851	<i>Gregarina Balani</i>	Diesing	1851: 10
1859	<i>Gregarina Balani</i>	Diesing	1859: 728
1863	<i>Gregarina Balani</i>	Lankester	1863: 95
1899	<i>Gregarina balani</i>	Labbé	1899: 36
1903	" <i>Gregarina</i> " <i>balani</i>	Minchin	1903: 329
1912	<i>Pyxinoides balani</i>	Trégouboff	1912: liii

Sporonts associated in pairs, ovoidal to cylindrical. Max. length seen by Kölliker 63μ , by Trégouboff 130μ primitive, 60μ satellite. Ratio LP : TL :: 1:1.3 to 1:3; WP : WD :: 1:1 to 1:1.4. Protomerite dome-shaped, slightly dilated below middle, terminating in a long cone upon which is surmounted an epimerite in the form of a short stylet dilated centrally into a bulb (Kölliker). Deep constriction at septum, deutomerite widest in middle. Nucleus larger, spherical with one karyosome.

Intestine of *Balanus pusillus* Ecker; *B. tintinnabulum* L. (Köll.), *B. amphitrite* Darw., *B. eburneus* Gould (Trég.).

Taken at Triest, Cete, France.

Kölliker first described this species, although he credits "Professor Ecker" with having seen it before, evidently without placing it upon record.

Frantzius reasonably considered it a member of the genus *Stylorhynchus* from the character of the epimerite, which resembles that of a new genus *Bulbocephalus* Watson (1916) of the family *Stylocephalidae*.

The species was not described again until the time of Trégouboff, who contributes many new observations, assigning to it a new name, evidently ignorant of the earlier work, and creating for it a new genus, *Pyxinoides*.

From the beautiful drawing of Kölliker, of a cephalont, there can be no doubt that one and the same species is involved. He even shows in the tiny figure the longitudinal grooves in the bulb of the epimerite.

Members of the genus *Balanus* also harbor *Nematoides fusiformis*, very similar in some respects but yet regarded as a separate species. See discussion under that species.

PYXINOIDES CTHAMALI (Léger and Duboscq) Trégouboff

[Figures 78 and 81]

1909	<i>Frenzelina cthamali</i>	Léger and Duboscq	1909a: 112, 114, 115
1911	<i>Frenzelina cthamali</i>	Sokolow	1911: 281
1912	<i>Pyxinoides cthamali</i>	Trégouboff	1912: lviii

Sporonts regularly cylindrical, primitive 230μ in max. length, satellite 170μ . Ratio LP : TL :: 1 : 4.5; WP : WD :: 1. 1. Protomerite wid-

est below mid-region, with characteristic specialized crescentic zone at apex, with what appears to be a canal leading from apex a short distance into protomerite. Deutomerite cylindrical, blunt at posterior end. No constriction at septum. Nucleus ovoidal with one large karyosome. Development extracellular. Epimerite atypical for that of the genus, but still Pyxinia-like, a long style reaching in large trophozoites to base of the cell and having a large crenulated cup-like enlargement at its midpoint, the rim of the cup being turned away from the body of the gregarine.

Cysts spherical, 85 to 100 μ in diameter. Spores unknown.

Intestine of *Cthamalus stellatus* Ranzani.

Taken at Cette, France.

In the first mention of the species, Léger and Duboscq 1909:112, the spelling is given as *chtamali* and that of the host genus *chtamalus*, while on pp. 114 and 115 the spelling is *chthamali* and *chthamalus*. Trégouboff gives it for both parasite and host as *chthamali* (*us*).

Family CEPHALOIDOPHORIDAE Kamm 1922

Intestinal parasites of Crustacea, development intracellular, early syzygies of two sporonts. Cysts without sporeducts, spores ovoidal with equatorial line. Entire life cycle passed within a single host.

DISCUSSION OF THE NEW FAMILY CEPHALOIDOPHORIDAE

The genus *Cephaloidophora* was created in 1908 by Mawrodiadi for intestinal parasites of the Crustacea. Léger and Duboscq in 1907 created a genus in all respects identical with the former genus naming it *Frenzelina*; but in 1911 they discovered that the name *Frenzelina* was preoccupied, so the name *Cephaloidophora* becomes the accepted genus designation.

The genus *Frenzelina* had been placed with the Gregarinidae because of the precocious association of sporonts in pairs; but there the similarities stop. *Cephaloidophora* was placed in the family *Stenophoridae* (Sokolow 1911:286) and it must be acknowledged that there are many characters in common with that family, including (a) intracellular development, (b) rudimentary epimerite, (c) spores ovoidal with equatorial line, (d) cysts without spore-ducts, (e) spores not united in chains. (A) is confined to these two groups alone, in both of which there is cell-destruction, all other known forms possessing extracellular trophozoitic stages without or with but little injury to the host. The only important variance in the two groups lies in the fact that the *Cephaloidophoridae* invariably form early syzygies of two individuals while the *Stenophoridae* as invariably do not. The shape of the body, usual shape and character of the nucleus and texture of the protoplasm are different in the two groups. For complications given below, the gregarines of the Crustacea should be considered apart from all others, at least until many of the knotty points

are cleared up by exhaustive researches. For these reasons I have raised the genus *Cephaloidophora* to a new family, Cephaloidophoridae.

Unlike other great groups of gregarines, the complete life-history of a crustacean parasite must be known before it can be assigned to a particular genus with a reasonable assurance of permanence; generally two out of three or four characters will determine the location of a gregarine. Unless the evolution of a sporozoite from the spore (Cephaloidophoridae) or from the cyst direct (Aggregatidae) is known and the intracellular development has been observed or proven to be absent, a crustacean parasite cannot be accurately placed. Léger and Duboscq, the closest students of the gregarines of the Crustacea, have removed many species hitherto classed as gregarines to the family Aggregatidae, now placed in the order Coccidia, because the sporozoites develop in the cyst without the intervention of spores. The sporogonic cycle of the Aggregatidae is passed in another host, a Cephalopod. Thus an alternation of hosts corresponds to an alternation of generations, the crab being eaten by the Cephalopod.

Another family of gregarines inhabiting Crustacea is the POROSPORIDAE, parasitic in Decapods only. These animals are very large, usually but not always solitary in the adult and are capable of forming cysts from a single individual. This raises the question that such cysts are schizogonic cysts and that the sporogonic stage, which possibly has not been seen, is passed in another host.

Léger and Duboscq (1911:lix) offer this hypothesis:

. . . . si *Cephaloidophora* et *Porospora* ne tomberont pas en synonymie, *Porospora* représentant la schizogonie et *Cephaloidophora* la gamogonie d'un même cycle.

Trégouboff (1912) says, however:

Je suis convaincu que les *Cephaloidophora* effectuent leur cycle dans un seul hôte et présentent un seul type des germes.

Minchin (1912:340) says:

A character such as the power of multiplication by schizogony is clearly one of great adaptive importance in the life-history of a parasitic organism, and therefore not likely to be of classificatory value. The classification of the future will probably be one which divides all gregarines into Cephalina and Acephalina, and distributes the Schizogregarines (into which suborder the Porosporidae are now placed) amongst these two divisions.

I think the last statement holds the clue to the classification of these puzzling forms. Léger and Duboscq first placed two of their early forms *Cephaloidophora fossor* and *C. ocellata* among the Aggregatidae, finding only coelomic cysts. After more exhaustive researches they found a life-history typically that of the genus *Cephaloidophora*, and removed the species to this genus, considering that the coelomic cysts they had previously found belonged to different gregarines, of which nothing else was known. I feel certain the latter really belonged in the same life-cycle and that the power of producing coelomic cysts and their concomitant

sporozoites within the original host is one means the parasite has of "holding its own" in Nature and reproducing at an enormous rate upon certain occasions. This migration of the young gregarine through the intestinal epithelium and production of a cyst from a single individual resulting in schizogonic sporozoites may be due to a change of food in the host animal unadapted to the parasite's requirements, to sickness of the host, to a scarcity of food, to the time of the year, or to a natural phenomenon occurring at stated intervals in the economy of the organism itself. Or it may be due to some extraneous cause not mentioned.

I am convinced that all the gregarines in the Crustacea will again come under one family head and that the Aggregatidae, the oldest known group, will be restored to its position among the gregarines. The Porosporidae and Cephaloidophoridae will of necessity be dropped. But in the meantime, until much more work on the crustacean parasites shall have been done and complete life-histories become the rule rather than the exception, the present group headings must remain.

Type Genus CEPHALOIDOPHORA Mawrodiadi 1908: 101

Intestinal parasites of Crustacea. Characters of the family.

CEPHALOIDOPHORA CONFORMIS (Diesing) Léger and Duboscq

[Figures 66 and 75]

1787	Unnamed	Cavolini	1787: 169
1810	? Distome	Rudolphi	1810: 287
1819	? Distome	Rudolphi	1819: 197
1851	<i>Gregarina conformis</i>	Diesing	1851: 15
1859	<i>Gregarina conformis</i>	Diesing	1859: 735
1863	<i>Gregarina conformis</i>	Lankester	1863: 95
1885	<i>Gregarina conformis</i>	Frenzel	1885: 579
1899	<i>Aggregata conformis</i>	Labbé	1899: 6
1903	<i>Aggregata conformis</i>	Minchin	1903: 331
1907	<i>Frenzelina conformis</i>	Léger and Duboscq	1907: 773
1908	<i>Frenzelina conformis</i>	Léger and Duboscq	1908: 99
1909	<i>Frenzelina conformis</i>	Léger and Duboscq	1909: 733
1909	<i>Frenzelina conformis</i>	Léger and Duboscq	1909a: 113
1911	<i>Frenzelina conformis</i>	Sokolow	1911: 280
1911	<i>Cephaloidophora conformis</i>	Léger and Duboscq	1911: lix
1913	<i>Aggregata conformis</i>	Ellis	1913: 264

(Frenzel) Sporonts associated in pairs, not more than two, irregularly cylindrical, tapering slightly, well-rounded posteriorly. Often a slight shoulder exists. Protomerite broadly dome-shaped, slightly constricted

at septum. 400 to 500 μ in length. Ratio LP:TL::1:6 (primate) 1:8 (satellite). WP:WD::1:5. Protomerite clear with large chromidial inclusions and crescentic apical area. Deutomerite dense, nucleus not seen in vivo, spherical, one or more karyosomes.

Cysts 150 μ in diameter. Spores ellipsoidal with faint equatorial line, 6.4 by 5 μ .

Intestine and gastric caeca of *Pachygraspus marmoratus* Fabr. (*Cancer depressus*).

Taken at Cavaliere, France, Naples, etc.

This is recognized as the earliest known species of Gregarines. Redi in 1708 found a parasite in the crab *Cancer pagurus* but Léger and Duboscq (1908) say:

La courte description et les images que Redi (1708) donne des vers du *Cancer pagurus* ne peuvent s'appliquer aux Gregarines des Crustacés, dont la découverte revient à Cavolini, quoiqu'en aient pensé Diesing (1851) et Labbé (1899).

Cavolini in 1787 discovered in "*Cancer depressi*" a parasite which he did not name and which Rudolphi (1810 and 1819) placed among his "vermes generis dubii," suggesting that it may be a Distome.

Diesing (1851) named the parasite *Gregarina conformis*. In the same paper he named another species seen by the same earlier workers *Gregarina praemorsa*. Hence either species might with equal right be named the type species. Diesing (1859) remarks only "Individua solitaria (Cavolini)."

Frenzel studied the species at length and gives several figures. The above description is taken mostly from his work.

Léger and Duboscq studied it again and find in their specimens that the satellite is the longer, while the primate is short and relatively stouter. The nucleus in their specimens is subspherical to ovoidal. Dimensions of the two descriptions compare favorably, an association given by the later workers as 1050 μ in length, 400 μ for the primate, the former being 80 μ wide and the latter 40 μ . Ratios of drawing of the latter's work are as follows: LP:TL::1:9 (primate) 1:21 (satellite); WP:WD::1:1.5 to 1:1.2. Thus their specimens conform to the type.

In 1907 these workers report schizogonic stages encountered in the coelom. They also found sporogonic encystment in the intestine with cysts 150 μ in diameter found in the excrement and two sizes of spores, 6.4 by 5 μ and microspores 5 μ by 4.7 μ .

CEPHALOIDOPHORA COMMUNIS Mawrodiadi Type Species

[Figure 77]

1890-1	No name	Solger	1890-1: 233
1899	<i>Gregarina</i> sp.	Labbé	1899: 36
1903	<i>Gregarina</i> sp.	Minchin	1903: 329
1908	<i>Cephaloidophora communis</i>	Mawrodiadi	1908: 101
1911	<i>Cephaloidophora communis</i>	Sokolow	1911: 286
1912	<i>Cephaloidophora communis</i>	Mercier	1912a: xli
1912	<i>Cephaloidophora communis</i>	Trégouboff	1912: liii

Sporonts 65-80 μ in length. Protomerite and deutomerite rounded. Associations in pairs, the primate the larger. Intracellular trophozoites found in intestinal epithelium and hepatic cells. A thickened hyalin crescentic area at apex of protomerite corresponding to a rudimentary epimerite. Ratio LP:TL::1:4; WP:WD:1:1.5. Cysts spherical. Spores with eight sporozoites, ovoidal, 4.5 by 4 μ , with faint equatorial line. Sporozoites subspherical

Hosts: *Balanus improvisus* Darw.; *B. improvisus gryphica* Münter; *B. tintinnabulum communis* L.; *B. perforans* Brug.; *B. amphitrite* Darw.; *B. eburneus* Gould.

Habitat: Intestine and caeca.

Taken at Odessa, Cette, France, etc.

The original description is in Russian and is not available. The above data is taken from Sokolow's translation and from Trégouboff's new observations upon live material.

Buddington (1910:470) gives a brief description of an unnamed species found in *Balanus eburneus* Gould, presumably at Woods Hole, Mass., merely stating the animal to be a polycystid gregarine of rapid movement, with a nucleus having five karyosomes and chromidial bodies in the protomerite. It is quite probable that he found the above species.

CEPHALOIDOPHORA FOSSOR (Léger and Duboscq) Trégouboff

[Figure 79]

1901	<i>Aggregata coelomica</i>	Léger	1901: 1343
1903	<i>Aggregata coelomica</i>	Léger and Duboscq	1903: cxlvii
1907	<i>Frenzelina fossor</i>	Léger and Duboscq	1907: 774
1908	<i>Frenzelina fossor</i>	Léger and Duboscq	1908: 99
1909	<i>Frenzelina fossor</i>	Léger and Duboscq	1909a: 112, 114, 115
1911	<i>Frenzelina fossor</i>	Sokolow	1911: 280
1912	<i>Cephaloidophora fossor</i>	Trégouboff	1912: lv
1912	<i>Cephaloidophora fossor</i>	Mercier	1912: xlv

Sporonts 150 μ in length. Ratio LP:TL::1:3 to 1:4; WP:WD::1:1.1. Sporonts obese, primate larger than satellite. Protomerite of primate broadly dome-shaped, twice as broad as high, with cres-

cent at anterior end and an apparent pore at the apex. Very slight constriction at the septum. Deutomerite ovoidal, broadly rounded at the distal end. Nucleus apparently ovoidal, situated near septum. Satellite more nearly cylindrical than primate.

Intracellular stage noted.

Intestine, coelom, and "sub-epithelium" of *Pinnotheres pisum* Penn.

In the first paper above, Léger reports finding coelomic schizogonic cysts 150μ in diameter which produce sporozoites directly.

Léger and Duboscq (1907) conclude that the two types of cysts encountered respectively in the coelom and alimentary tract represent different species of parasites, only one type of sporont having been seen, however. They have found no other stages of the coelomic gregarine except the cysts and contained sporozoites and have found all the stages in the life-history of the intestinal parasite. I am convinced that but one species is involved producing two kinds of cysts depending on conditions not yet determined. I am not ready, however, to remove any of the species now placed to another position. Much more work is needed upon crustacean gregarines and parasites placed elsewhere before any species can be assigned positions with a fair degree of permanence.

CEPHALOIDOPHORA OCELLATA (Léger and Duboscq) Kamm

[Figure 80

1903	<i>Aggregata vagans</i>	Léger and Duboscq	1903: cxlvii
1907	<i>Frenzelina ocellata</i>	Léger and Duboscq	1907: 774
1908	<i>Frenzelina ocellata</i>	Léger and Duboscq	1908: 99
1909	<i>Frenzelina ocellata</i>	Léger and Duboscq	1909a: 112, 114, 115
1911	<i>Frenzelina ocellata</i>	Sokolow	1911: 280-1
1922	<i>Cephaloidophora ocellata</i>	Kamm	1922 (this paper)

Sporonts in pairs, elongate cylindrical, 200μ in maximum length. Primate the larger. Ratio LP:TL :: 1:6 to 1:9; WP:WD :: 1:0.9. Protomerite widest anterior to the mid-region with two large corpuscles resembling eyes in both primate and satellite. A flattened cone projects at the anterior end. Slight constriction at septum. Deutomerite widest at shoulder, tapering from thence gradually and terminating in a broadly rounded end. Nucleus ovoidal to rectangular, situated at or above mid-region of deutomerite.

Intestine of *Eupagurus Prideauxi* Leach.

Taken at Banyuls, France.

This species was first described as *Aggregata vagans* and shown to exist during the sporont stage in the intestine but to be able to pass while comparatively large in size through the epithelium into the coelom. A single individual here swells, its protoplasm changes in character, and it finally becomes a schizogonic cyst 150μ in diameter in which are produced sporozoites directly, as in the family Aggregatidae.

Typical sporont cysts are also noted in the excrement from the alimentary tract.

The authors think that the two kinds of sporozoites represent different species of parasites, the sporogonic representing the new species, *Frenzelina occlata*. I am of the opinion that but one species is involved. See discussion under *Cephaloidophora fossor* and also Discussion of the New Family Cephaloidophoridae, at the beginning of Crustacean Parasites.

CEPHALOIDOPHORA MACULATA Léger and Duboscq

[Figure 68]

1911	<i>Cephaloidophora maculata</i>	Léger and Duboscq	1911 : lix
1912	<i>Cephaloidophora maculata</i>	Trégouboff	1912 : liv
1912	<i>Cephaloidophora maculata</i>	Mercier	1912a: xliii

Sporonts small, ovoidal, maximum length 80 μ . Ratio LP : TL :: 1 : 4 to 5; WP : WD :: 1 : 1.5 to 2. Cytoplasm yellowish in deutomerite, clear in protomerite. Spherical chromidial bodies in protomerite. Nucleus small, spherical, one karyosome. Characteristic crescentic apical area in protomerite. Cysts spherical, 100 μ in diameter. Spores spherical to subspherical, 4 μ in diameter, with equatorial line. Intracellular stage observed.

Intestine of *Gammarus marinus* Leach.

Taken at Roscoff, France.

CEPHALOIDOPHORA TALITRI Mercier

[Figure 86]

1912	<i>Cephaloidophora talitri</i>	Mercier	1912: 38
1912	<i>Cephaloidophora talitri</i>	Mercier	1912a: xliv
1912	<i>Cephaloidophora talitri</i>	Trégouboff	1912: lv

Sporonts in pairs, primitive the larger, ovoidal, average length 40 μ . Ratio LP : TL :: trophozoites 1 : 4.5 to 6; WP : WD :: 1 : 1.2 to 2. Protomerite dome-shaped with rudimentary epimeritic area at apex. Slight constriction at septum. Deutomerite broadly ovoidal, nucleus spherical with one large karyosome. Intracellular stage noted.

Cyst and spores unknown.

Intestine of *Talitrus saltator* Mont.

Taken at Roscoff, France.

CEPHALOIDOPHORA OLIVIA (Watson) Kamm

[Figure 83]

1912	<i>Frenzelina olivia</i>	Watson	1916: 133
1922	<i>Cephaloidophora olivia</i>	Kamm	1922 (this paper)

Sporonts in pairs, max. length association 218 μ , ellipsoidal, largest sporont 118 by 36 μ . Ratio LP : TL :: 1 : 5. WP : WD :: 1 : 1.3.

Protomerite dome-shaped, constriction at septum slight, papillate area at apex of protomerite orange in color. Deutomerite long-ovoidal. Nucleus spherical, one karyosome. Cysts spherical, 60μ . Spores unknown.

Intestine of *Libinia dubia*.

Taken at Cold Spring Harbor, Long Island.

CEPHALOIDOPHORA NIGROFUSCA (Watson) Kamm

[Figure 84]

1912 <i>Frenzelina nigrofusca</i>	Watson	1916: 134
1922 <i>Cephaloidophora nigrofusca</i>	Kamm	1922 (this paper)

Sporonts stout-bodied, ovoidal to rectangular, maximum size 125μ by 75μ . LP:TL::1:4; WP:WD::1:1.5. Protomerite broadly dome-shaped with characteristic papillate apical area. Slight constriction at septum. Deutomerite regularly cylindrical, broadly-rounded at posterior end. Protoplasm very dense. Nucleus small, spherical with one or two karyosomes.

Cysts and spores unknown.

Hosts: *Uca pugnax*, *Uca pugilator*. Intestine.

Taken at Cold Spring Harbor, Long Island.

CEPHALOIDOPHORA DELPHINIA (Watson) Kamm

[Figure 85]

1916 <i>Frenzelina delphinia</i>	Watson	1916: 29
1922 <i>Cephaloidophora delphinia</i>	Kamm	1922 (this paper)

Sporonts ovoidal, maximum length association 215μ , largest sporont 115 by 64μ . Ratio LP:TL::1:4; WP:WD::1:1.5. Protomerite irregularly dome-shaped, dilated medianly. Papillated apex. Very slight constriction at septum. Deutomerite ovoidal. Nucleus spherical, one karyosome.

Cysts spherical, 80μ . Spores unknown.

Intracellular stage noted.

Intestine of *Talorchestia longicornis* Say.

Taken at Cold Spring Harbor, Long Island.

CEPHALOIDOPHORA AMPELISCA (Nowlin and Smith) Kamm

[Figure 71]

1917 <i>Frenzelina ampelisca</i>	Nowlin and Smith	1917: 83
1920 <i>Cephaloidophora ampelisca</i>	Kamm	1922 (this paper)

Sporonts elongate cylindrical, 62μ by 15μ in maximum dimensions. Sporonts in pairs. Ratio LP:TL::1:6 to 1:9; WP:WD::1:1. Protomerite broadly dome-shaped, dilated in middle, more or less constricted at septum and possessing a rudimentary epimerite or broad

apical papilla. Several chromidial bodies in protomerite. Deutomerite cylindrical, blunt at posterior end. Nucleus spherical with one or more karyosomes.

Intracellular development noted.

Intestine and hepatic caeca of *Ampelisca spinipes*.

Taken at Woods Hole, Mass.

Genera of Uncertain Position

NEMATOIDES Mingazzini 1891 2nd sem.: 233

Dicystid, no septum in sporonts. Epimerite forked, at apex of a long neck. "Corpo allungato fusiforme, aguzzo ad entrambi gli apici. Cuticola liscia."

NEMATOIDES FUSIFORMIS Mingazzini Type Species

1891	<i>Nematoides fusiformis</i>	Mingazzini	1891: 2nd sem. 233
1899	<i>Nematoides fusiformis</i>	Labbé	1899: 34
1903	<i>Nematoides fusiformis</i>	Minchin	1903: 203, 329, 331

Characters of the genus. "Trophozoite vermiform, without septum. Epimerite in form of a fork or pair of pincers, borne on an elongated neck." Minchin.

Intestine of *Balanus perforatus*, *Pollicipes cornucopia*.

Balanus sp. also harbor *Cephaloidophora communis* Mawr. and *Pyxinoides balani* (Kölliker) Trégouboff.

Mingazzini says the new species above is the *Gregarina balani* of Kölliker. But the cephalont depicted by Kölliker corresponds in every particular with that of an early cephalont of *Pyxinoides balani*. See discussion under that species.

If, however, the fully developed epimerites of the two species, *Pyxinoides balani* and *Nematoides fusiformis* are considered, they are suspiciously similar. Labbé emends the original description of the latter thus:

Epim. en forme de fourche ou de pince,
séparé par un col allongé du reste du corps.

The only character, then, in which the two species differ is this: The latter possesses no septum in the sporont and is in appearance a Monocystid, while the former has a complete septum in all stages except the very earliest. Exhaustive researches may contribute something upon this point and prove the two species identical.

Below is the original description of the species:

Cercando nell'intestino del *Balanus perforatus* la *Gregarina balani* der Kölliker che è una policistidea, ho trovato invece una monocistidea appartenente a questo gruppo di gregarine vermiformi. È piuttosto lunga, ha la membrana intieramente liscia, un nucleo ovale al centro con un nucleolo. Sembra assai rara. L'apice anteriore, troncato, termina con una specie di ventosa, il posteriore invece è affatto puntuto. Nell'apice anteriore vi è un po'di metaplasma, nel resto vi ha l'endoplasma.

GANYMEDES Huxley 1910:55

A possible fixation organ at interior end, consisting of a motile stalked sphere. Cup at posterior end which fits into ball of a satellite. No septum, no true epimerite. Typical gregarinoid encystment, cysts spherical. Alimentary tract of Crustacea.

Huxley offers the hypothesis that this gregarine lies between the polycystids and the monocystids and creates for it a new family, Ganymedidae. Since his studies were made only upon fixed material and all characters of this very unusual parasite are unknown, I think the rank of a new family is hardly justifiable and prefer to consider it among the Genera of Uncertain Position.

GANYMEDES ANASPIDIS Huxley Type Species

[Figure 89]

1910	<i>Ganymedes anaspidis</i>	Huxley	1910: 155
1913	<i>Ganymedes anaspidis</i>	Ellis	1913: 264

Characters of the genus. Sporonts in pairs, elongate cylindrical, maximum length 200μ , width 120μ . Average size 250μ to 300μ by 17μ to 20μ . Nucleus large, ellipsoidal, one large karyosome. Cysts spherical, 100μ in diameter.

Anterior end of protomerite a "distinct stalked sphere," 8 to 10μ across. Protoplasm of anterior end highly specialized, posterior end a socket into which fits the "ball" of another individual, during the associative period.

Intestine and pyloric caeca of *Anaspides tasmaniae* (Thompson).

Taken on the Island of Tasmania.

Species of Uncertain Position

[? *gammari* von Siebold]

1839	<i>Gregarina gammari</i>	von Siebold	1839: ?
1848	<i>Gregarina Gammari?</i>	Frantzius	1848: 196
1848	? <i>Gregarina longissima</i>	Kölliker	1848: 35
1859	<i>Gregarina Gammari</i>	Diesing	1859: 735
1863	<i>Gregarina longissima</i>	Lankester	1863: 95
1886	<i>Gregarina Gammari</i>	Plate	1886: 236
1895	<i>Gregarina</i> sp.	Pfeiffer	1895: 60
1899	<i>Gregarina</i> sp.	Labbé	1899: 36
1903	<i>Gregarina</i> sp.	Minchin	1903: 330

Epimerite present. Sporonts 425μ in length, long-ovoidal.

Intestine and ? coelom of *Gammarus pulex*.

von Siebold described *Didymophyes longissima* from the same host, considering it a second form of the same species. In the same paper,

however, he described the above species from the same host, overlapping his first observations with two names.

Diesing (1859) refers to this species thus:

Receptaculum globosum. Corpus ovoideum receptaculo duplo longius. Longit crassit

He regards it as synonymous with the specimens seen by von Siebold and described by Kölliker as follows:

Neben dieser Gregarine fand v. Siebold in *Gammarus pulex* noch eine andere Form (Fig. 29c), von der es zweifelhaft bleibt, ob sie als Entwicklungsform zu der *Gr. longissima* zu rechnen ist oder nicht.

Kölliker's figure obviously represents an entirely different species which seems to correspond to one mentioned later in this discussion.

Lankester (1863) regards these as synonymous:

Gregarina longissima Sieb., *Gr. diffluens* Dies., *Gr. millaria* Dies., *Gr. putanea* Leuckart, *Gr. Gammari* Sieb.

Plate (1886) found in the intestine of *Gammarus pulex* two polycystid gregarines. One is small, elongate cylindrical, 255 in length, the other long-ovoidal, 425 μ in length. The one seems to correspond with *Didymophyes longissima* and the other with *Gregarina gammari*.

This species agrees in form and proportions with *Cephaloidophora maculata* from *Gammarus marinus* but sporonts of the present species attain 425 μ in length while those of the former reach only 80 μ .

Two species described by Diesing (1851:7) both from *Gammarus pulex* are sufficiently alike to be considered synonymous. No detailed description of the species (? *Gammari* von Sieb.) is extant and so they cannot be compared in minutae with the present species, but since all three are found in the same host they should obviously be considered together under the oldest name. These species are mentioned below

1851 *Gregarina millaria* Diesing 1851: 7

1859 *Gregarina millaria* Diesing 1859:731

Proboscis cylindrica gracilis, apice obtuse conica, uncinulorum seriebus 10-20. Receptaculum subglobosum papillosum. Corpus ellipticum turgidum receptaculo triplo longius, laete auranticum. Longit. $\frac{1}{2}$ "', crassit. . . .

Hosts: *Gammarus pulex*, *Astacus fluviatilis*. Intestine.

1851 *Gregarina diffluens* Diesing 1851: 7

1859 *Gregarina diffluens* Diesing 1859: 731

Proboscis cylindrica brevis gracilis, apice longe conica obtusa, uncinulorum seriebus 10-20. Receptaculum subglobosum papillosum. Corpus oblongum per intervalla coarctatum postice rotundatum, saturate auricatum, facillime diffluens. Longit. 1''' ; crassit. . . .

Host: *Gammarus pulex*.

[? sp. Mawrodiadi]

1908	No name	Mawrodiadi	1908: 101
1911	<i>Gregarina</i> sp.	Sokolow	1911: 287
1912	No name	Trégouboff	1912: lviii

Sporont 130-140 μ in length, same general form as *Pyxinooides balani* (Kölliker) Trégouboff, but with a long epimerite which penetrates to the muscular layer.

. . . la grégarine possède un long épimérite, qui traverse tout le tissu épithélial, s'accolle à la gaine musculaire sous-jacente et la suce. (Quoted by Trégouboff from Mawrodiadi.)

Trégouboff adds:

Il est impossible de juger même de la parenté entre ces deux Grégarines étant donné la déficuosité de la description qui d'ailleurs tient toute dans les quelques mots cités plus haut.

Intestine of *Balanus amphitrite pallidus* Darw., *B. amphitrite* Darw., *B. eburneus* Gould.

Taken in the Black Sea.

[? valettei Nussbaum]

1890	<i>Gregarina valettei</i>	Nussbaum	1890: 156
1899	<i>Gregarina valettei</i>	Labbé	1899: 36
1903	" <i>Gregarina</i> " <i>valettei</i>	Minchin	1903: 331
1912	<i>Gregarina valettei</i>	Trégouboff	1912: lvii

Epimerite a simple stylet. Sporont 58 μ in length.

Intestine of *Pollicipes polymerus* Sow.

Taken in California.

Trégouboff concludes

. . . cette Grégarine, . . . n'est certainement pas une *Gregarina sensu stricto*.

[? praemorsa Diesing]

1684	?	Redi	1684: 183
1729	?	Redi	1729: 270
1810	Distome or Monostome?	Rudolphi	1810: 287
1819	Distome or Monostome?	Rudolphi	1819: 197
1851	<i>Gregarina praemorsa</i>	Diesing	1851: 287
1859	<i>Gregarina praemorsa</i>	Diesing	1859: 735
1863	<i>Gregarina praemorsa</i>	Lankester	1863: 95
1899	<i>Aggregata praemorsa</i>	Labbé	1899: 6
1903	<i>Aggregata praemorsa</i>	Minchin	1903: 329
1908	<i>Frenzelina praemorsa</i>	Léger and Duboscq	1908: 99
1909	<i>Frenzelina praemorsa</i>	Léger and Duboscq	1909a: 112
1911	<i>Frenzelina praemorsa</i>	Sokolow	1911: 280
1922	<i>Cephaloidophora</i> (?) <i>praemorsa</i>	Kamm	1922 (this paper)

Intestine and "ovarian appendage" of *Cancer pagurus* L. (*Platycarcinus* (Lankester)).

The first reference in literature to what may possibly have been a gregarine was that of Redi in 1684, who found in the "vesicular ovariorum" of *Cancer paguri* a parasite which Rudolphi (1810, 1819) refers to as a possible Distome or Monostome, and places in a list of "Vermes generis dubii."

Diesing (1851) named the species *Gregarina praemorsa* from the originally observed material and contributes no new observations. In 1859 he merely reports "Individua solitaria (Redi)."

As stated under *Cephaloidophora conformis*, Léger and Duboscq (1908) do not credit Redi's observations as referring to authentic gregarines but give to Calvolini (1787) the honor of having first seen and recorded undoubted specimens of this group. Rudolphi does not mention Cavolini in connection with the present species, however.

Léger and Duboscq (1908 and 1909a) merely mention the species by name in a list with this heading:

Le genre Frenzelina comprend ainsi actuellement les especes suivantes:

Sokolow lists it with the authentic species of the genus Frenzelina, not with a group of uncertain species.

Thus there is no record of positive data concerning the actual existence of this parasite as a gregarine. No description or drawing is extant. It is remarkable that the mere reference has held its place in literature for over two hundred years.

[? clausii Frenzel]

[Figure 69]

1879	?	Claus	1879: 78
1885	<i>Gregarina Clausii</i>	Frenzel	1885: 575
1899	<i>Gregarina clausi</i>	Labbé	1899: 37
1903	" <i>Gregarina</i> " <i>clausi</i>	Minchin	1903: 331

Sporonts solitary, ovoidal, 100μ in maximum length. Ratio LP: TL :: 1:5.5; WP:WD :: 1:1.5. Epimerite unknown. Protomerite domeshaped, striated longitudinally. Deutomerite widest at shoulder, tapering to a rounded point. No constriction at septum. Chromidial bodies in protomerite. Nucleus spherical.

Solitary encystment within two thick hyalin cyst-walls. Cysts and spores not described.

Intestine of *Phronima* sp., *Phronimella* sp.

Taken at Naples.

The position of this species cannot be determined from the known data. Inclusion within the Cephaloidophoridae is doubtful from the solitary encystment.

[? nicaeae Frenzel]

[Figure 70]

1885	<i>Gregarina Nicaeae</i>	Frenzel	1885: 578
1899	<i>Aggregata nicaeae</i>	Labbé	1899: 6
1903	<i>Aggregata nicaeae</i>	Minchin	1903: 330

Sporonts associated in pairs. Length 60μ . Ratio LP : TL :: 1 : 3 to 4; WP : WD :: 1 : 1. Protomerite dome-shaped, deutomerite tapering to a blunt point. No constriction at septum. Nucleus large, spherical, 15μ in diameter.

Cyst and spores unknown.

Intestine of *Hyale pontica* Rathke (*Nicaea Nilsonii*).

Taken at Naples.

There is an equal possibility of this species belonging with the Cephaloidophoridae and with the Aggregatidae from the characters recorded. The exact position can only be determined after cyst and spores (or their absence) are demonstrated.

[? sp. Minchin]

1903 Septate Gregarine Minchin 1903: 330
 "Original observation."
 Intestine of *Nebalia serrata*.
 No comment whatever is offered concerning this parasite.

LIST OF SPECIES FOUND IN THE CLASS ACERATA

PARASITE	HOST
ACTINOCEPHALIDAE	
<i>Anthorhynchus sophiae</i> (Schneider) Labbé	<i>Phalangius opilio</i>
Type species	
<i>Sciadophora phalangii</i> (Léger) Labbé	<i>Phalangium crassum</i>
Type species	<i>P. cornutum</i>
	<i>Opilio grossipes</i> Herbst.
<i>Sciadophora fissidens</i> (Rössler) Labbé	<i>Phalangidae</i> sp.
<i>Sciadophora caudatus</i> (Rössler) Kamm	<i>Phalangidae</i> sp.
<i>Sciadophora goronowitschi</i> (Johansen) Labbé	<i>Phalangium opilio</i>
ACANTHOSPORIDAE	
<i>Acanthospora repelini</i> Léger	<i>Phalangium cornutum</i>
	<i>P. opilio</i>
UNCERTAIN SPECIES	
[? Wellmer]	<i>Oribata geniculata</i> (L.)
Not named Sokolow]	<i>Scorpio indicus</i>

Family ACTINOCEPHALIDAE Léger 1892: 166

Sporonts solitary, epimerites complex and varied. Cyst dehiscence by simple rupture, spores irregular, biconical, or cylindro-biconical.

Genus ANTHORHYNCHUS Schneider 1887: 69, emend Labbé 1899: 19

Epimerite a large flattened and fluted button, spores ovoidal, knobbed at sides, united in chains laterally.

ANTHORHYNCHUS SOPHIAE (Schneider) Labbé Type Species

[Figures 58, 108]

1887	<i>Anthocephalus Sophiae</i>	Schneider	1887: 69
1897	<i>Anthocephalus Sophiae</i>	Léger	1897: 11
1899	<i>Anthorhynchus Sophiae</i>	Labbé	1899: 19
1903	<i>Anthorhynchus Sophiae</i>	Minchin	1903: 199, 338
1913	<i>Anthorhynchus Sophiae</i>	Ellis	1913: 279

Sporonts solitary, obese. Maximum length 2 mm. Width protomerite 330 μ , deutomerite 600 μ . Ratio LP:TL::1:11 (without epimerite); WP:WD::1.2. Protomerite small, flattened, three times as wide as high, no constriction at septum. Deutomerite conoidal, widest just below septum, tapering thence and ending in a broad blunt extremity. Epimerite a series of short blunt digitiform processes united laterally and curved inward to form a broad flattened corona. Epimerite 200 μ high. Nucleus not described.

Spores 6.9 by 4.6 μ , broad, biconical, extruded in chains laterally attached.

Intestine of *Phalangium opilio*.

Taken at Poitiers, France.

Genus SCIADOPHORA Léger 1897: 36, emend Labbé 1899: 18

Epimerite a large flattened centrally indented papilla with a crenulate periphery. Protomerite with numerous backwardly directed leaf-like processes arranged vertically, each sharply pointed at its posterior extremity.

SCIADOPHORA PHALANGII (Léger) Labbé Type Species

[Figures 59, 60, 62, and 106]

1897	<i>Lycosella Phalangii</i>	Léger	1897: 12, 36
1899	<i>Sciadophora phalangii</i>	Labbé	1899: 18
1903	<i>Sciadophora phalangii</i>	Minchin	1903: 199, 338
1911	<i>Sciadophora phalangii</i>	Wellmer	1911: 127
1913	<i>Sciadophora phalangii</i>	Ellis	1913: 280

Sporonts solitary, very elongate, up to 2.5 mm., one of the largest known species. Width not given. Ratio LP:TL::1:12; WP:WD::1.3:1. Protomerite broadly conical at apex with 15 or 16 vertical lamillar plates starting below the apical cone recurving backward and terminating in sharp hooks. The whole bears a resemblance to an umbrella. Deep constriction at septum. Deutomerite widest at shoulder, tapering to a very long slender acuminate extremity. Epimerite a large

nearly sessile papilla indented in middle and crenulate on periphery. Nucleus ovoidal, nearly spherical, with many karyosomes.

Cysts spherical, $\frac{1}{2}$ mm., dehiscence by simple rupture, spores biconical but rounded off at poles. Unique. $9 \times 5\mu$.

Intestine and caeca of *Phalangium crassum*, *P. cornutum*, *Opilio grossipes* Herbst.

Taken in Provence, France and East Prussia.

Two species have been described previous to this one and considered by Léger as synonymous; I have, however, not considered them so. They are incompletely described but quite different from the type species and because of the regularity of the digitiform bifurcate processes may not belong in the genus. This is what Léger says concerning the species:

. . . . sans rien préjuger des espèces observées par M. Johansen et M. Rössler, je donne à celle que j'ai étudiée le nom spécifique de *Lycosella phalangii* qui indique son origine. Il ne paraît pas douteux cependant que, d'après leurs caractères morphologiques, les deux grégaires signalées par ces auteurs appartiennent au genre *Lycosella* et soient des espèces très voisines de celle que je décris dans ce travail, c'est ce que l'étude complète de leur cycle viendra nous confirmer un jour ou l'autre.

SCIADOPHORA FISSIDENS (Rössler) Labbé

[Figures 110 and 111]

1882	<i>Actinocephalus fissidens</i>	Rössler	1882: 700
1897	<i>Lycosella Phalangii</i>	Léger	1897: 12, 36
1899	<i>Sciadophora fissidens</i>	Labbé	1899: 18
1903	<i>Sciadophora fissidens</i>	Minchin	1903: 338

Sporonts solitary, 2 to 3 mm. in length. Ratio LP:TL::1:8; WP:WD::1:1.5. The protomerite is broadly dome-shaped, at the mid-region there is developed a corona of processes directed gently backward in two rows, the upper consisting of twelve long sharp spines, the lower of twelve broad plates widest at the middle and bifurcate at the ends, superficially resembling a lobster's claw. These are arranged alternately with the spines of the upper row. (Fig. 111). Deutomerite widest at shoulder, tapering gently backward, the posterior third, however, being a very much narrowed cylinder. Nucleus small, spherical.

Intestine and caeca of *Phalangidae* sp.

Taken at Freiburg, Germany.

This peculiar parasite in appearance is very unlike the type species, (Cf. Figs. 62 and 110) but because the crenulations are a part of the protomerite and not an epimerite, must be placed in this genus, or in a yet undescribed genus very similar. The complete life-history remaining unsolved, the species is placed here tentatively.

Rössler describes the peculiar protuberances thus:

. . . . zeigt am Kopf zwölf gespaltene Hakenpaare und zwischen je zweien dieser Paare einen einfachen, stachelförmigen Dorn.

SCIADOPHORA CAUDATUS (Rössler) Kamm

[Figures 112 and 113]

1882	<i>Stylorhynchus caudatus</i>	Rössler	1882: 700
1899	<i>Stylorhynchus caudatus</i>	Labbé	1899: 33
1903	<i>Stylorhynchus caudatus</i>	Minchin	1903: 338
1913	<i>Stylocephalus caudatus</i>	Ellis	1913: 338
1922	<i>Sciadophora caudatus</i>	Kamm	1922 (this paper)

Sporonts solitary, 2 to 2.5 mm. with a long "tail-process" 2 to 3 mm. in addition. This makes the species the longest known gregarine. Body similar in shape to *S. fissidens* except for the tail. The protomerite is situated upon a short neck with a dome-shaped top and a corona of twelve digitiform processes at the mid-region. Nucleus spherical.

Intestine and caeca of Phalangidae sp.

Taken at Freiburg, Germany.

This species and the preceding one are differentiated by the character of the protomeritic corona. Cf. Figs. 111 and 113. It is evident that they belong to the same genus, for the corona of each is a part of the protomerite rather than of an epimerite. Rössler considers the fact that this species possesses a long neck upon which is superimposed the protomerite sufficient evidence to place it in the genus *Stylocephalus*, but the coronae are so similar and the host identical—the two found in the same intestines—leads one to suspect that the two forms may represent parts of a single life-history. Further investigations are, however, necessary to establish this statement or refute it.

Rössler says concerning the species:

. . . besitzt einen gestielten Kopf, der mit zwölf Erhebungen oder Leisten versehen ist, die über den Rand desselben hinausragen und sich theilen. Diese Form ist ausserdem mit einem dünnen, schwanzartigen Anhang versehen der durch keine Scheidewand von dem eigentlichen Körper getrennt ist, jedoch auch keine einspringenden Konturen zeigt, die auf einen verstückelten Zustand schliessen liessen.

SCIADOPHORA GORONOWITSCHI (Johansen) Labbé

[Figures 104 and 105]

1894	<i>Actinocephalus Goronowitschi</i>	Johansen	1894: 140
1897	<i>Lycosella Phalangii</i>	Léger	1897: 11, 36
1899	<i>Sciadophora goronowitschi</i>	Labbé	1899: 18
1903	<i>Sciadophora goronowitschi</i>	Minchin	1903: 338

No dimensions or complete figure are given. Johansen describes the peculiar parasite thus:

. . . näher zum Deutomerit gelegenen Äquator eine Reihe von Häckchen und Dörnchen zur Befestigung des Parasiten an dem Gewebe der Phalangide dient.

His meagre illustration, Fig. 105, indicates a bifurcation of the processes, as in the species found by Rössler.

Maximum length 5 mm. This length is reached only by the species just preceding, the two being the longest known species of gregarines.

Intestine of *Phalangium opilio*.

Taken at Tomsk, Russia.

Léger also found *Acanthospora repelini* in his material.

Family ACANTHOSPORIDAE Léger 1892: 167

Sporonts solitary. Epimerite simple or appendicular. Dehiscence by simple rupture. Spores with equatorial and polar spines.

Genus ACANTHOSPORA Léger 1892: 167

Epimerite a simple large conical papilla on a short neck. Spores biconical or ovoidal with a row of equatorial spines and a tuft of four spines at each pole.

ACANTHOSPORA REPELINI Léger

[Figures 57 and 107]

1897	<i>Acanthospora Repelini</i>	Léger	1897: 13, 42
1899	<i>Acanthospora repelini</i>	Labbé	1899: 28
1903	<i>Acanthospora repelini</i>	Minchin	1903: 338
1911	<i>Acanthospora repelini</i>	Wellmer	1911: 139

Sporonts solitary, obese. Maximum length 1 mm., width 250 μ . Ratio LP : TL :: 1 : 4 (without epimerite); WP : WD :: 1 : 1.2. Proto-merite dome-shaped, deeply constricted at septum. Deutomerite widest in anterior third, tapering irregularly to a sharp point. Epimerite a broad flattened papilla indented in the middle and crenulate along the margin. Nucleus spherical, one karyosome.

Cysts spherical, 500 μ , dehiscence by simple rupture. Spores 13 by 4.8 μ , biconical, spines at apices and equator.

Intestine of *Opilio grossipes* Herbst, *Phalangium cornutum*, and *P. opilio*.

Taken in Tourraine, France, and in East Prussia.

This species was found in association with *Sciadophora phalangii* by Léger. There is no possibility of confusion, however, in the two species.

The epimerite of this species does not conform closely to that of the type, *A. pileata* (Léger, 1892: 115).

Uncertain Species

[? Wellmer]

1911	<i>Gregarina</i> sp.	Wellmer	1911: 148
	Intestine of <i>Oribata geniculata</i> (L.). Taken in East Prussia.		
	There are no data whatever concerning this gregarine form.		

		[? Sokolow]	
		[Figure 109]	
1908	Not named	Sokolow	1908: 500
1911	Not named	Sokolow	1911: 295

33 μ in length. Nucleus spherical, 3 μ . Seen in copulation.
Host: *Scorpio indicus*.
No other data are given concerning this gregarine form.

SPECIES FOUND IN THE CLASS MALACOPODA
SPECIES OF DOUBTFUL POSITION

[? Moseley]			<i>Peripatus capensis</i> Grube
		[? Moseley]	
1874	" <i>Gregarinae</i> "	Moseley	1874: 762
1899	<i>Gregarina</i> sp.	Labbé	1899: 37
1903	<i>Gregarina</i> sp.	Minchin	1903: 331

The only data which exist concerning this parasite are the following:

Some very small encysted *Gregarinae* were found in the stomachs of all the specimens examined.

Host: *Peripatus capensis* Grube.

Taken in Equatorial Africa.

One might wish that more data existed concerning the type of gregarine which inhabit this intermediate host. Theoretically, it should be a form intermediate between the family Polyrhabdinidae and the true Cephaline Gregarines.

LIST OF SPECIES FOUND IN THE ORDER THYSANURA OF THE CLASS
HEXAPODA

PARASITE	Host
GREGARINIDAE	
<i>Gregarina lagenoides</i> (Léger) Labbé	<i>Lepisma saccharina</i> L.
SPECIES OF DOUBTFUL POSITION	
? <i>Gregarina podurae</i> (Léger) Labbé	<i>Podura villosa</i>
<i>Gregarina</i> sp. Wellmer	<i>Sminthurus fuscus</i> L.

Family GREGARINIDAE Labbé 1899: 9

Genus GREGARINA Dufour 1828: 366

Sporonts in pairs, epimerite a small sessile knob or cone. Spores barrel-shaped to cylindrical. Cysts with spore ducts.

GREGARINA LAGENOÏDES (Léger) Labbé

[Figure 52]

1892	<i>Clepsidrina Lagenoïdes</i>	Léger	1892: 118
1899	<i>Gregarina lagenoides</i>	Labbé	1899: 11
1903	<i>Gregarina lagenoides</i>	Minchin	1903: 335
1911	<i>Gregarina lagenoides</i>	Wellmer	1911: 117

Sporonts in pairs, elongate. Length 150μ , width not given. Ratio LP : TL :: 1 : 3.5. WP : WD :: 1 : 1.3. Protomerite of primate cylindrical, with conical apex, the conical portion nearly equalling the cylindrical in length. Slight constriction at septum. Deutomerite constricted at end of anterior third, rapidly swelling to an almost perfect globe in posterior two-thirds. Satellite of practically same shape but less accentuated. Epimerite a simple spherical or ovoidal papilla.

Cysts spherical, dehiscing by spore-ducts, spores in chains. Spores biconical, blunt at poles.

Intestine of *Lepisma saccharina* L.

Taken in the Valley of the Creuse, France, and in East Prussia.

Species of Doubtful Position

? GREGARINA PODURAE (Léger) Labbé

[Figures 53 and 54]

1892	<i>Clepsidrina Podurae</i>	Léger	1892: 119
1899	<i>Gregarina podurae</i>	Labbé	1899: 12
1903	<i>Gregarina podurae</i>	Minchin	1903: 336

Sporonts in pairs or threes. Maximum length 90μ . Protomerite either separated from deutomerite by septum or lacking the septum. Ratio LP : TL :: 1 : 5.5; WP : WD :: 1 : 1.8. In normal individuals protomerite dome-shaped, flattened apically. No constriction at septum. Deutomerite cylindrical, broadly truncate at base.

In individuals which lack the septum the whole animal is ovoidal with or without a very small papillate epimerite. Normal epimerite much larger, a slightly stalked papilla. The individuals which form associations of more than two are of the abnormal ovoidal type.

The protoplasm is gray-green with large orange granules. The nucleus is spherical, with one karyosome.

Cysts spherical, 80μ , one long spore-duct, spores in chains, 6.8 by 3μ .

Intestine of *Podura villosa* and *Orchesella* sp.

Taken in the Valley of the Loire, France.

This species seems to be an aberrant one representing a transitory species to another genus or an intestine in which for some reason the gregarines became abnormal. The possibility of more than one species being present is excluded from the same type of protoplasm of peculiar color and texture in both kinds of individuals. The author suggests that the species may be intermediate between the genus *Gamocystis*, in which a septum is always absent, and *Gregarina* in which it is always present.

Gregarina sp. Wellmer1911 *Gregarina* sp. Wellmer 1911: 146

There are no data whatever concerning this form.

Intestine of *Sminthurus fuscus* L.

Taken in East Prussia.

LIST OF SPECIES FOUND IN THE ORDER ISOPTERA OF
THE CLASS HEXAPODA

SPECIES OF DOUBTFUL POSITION

? *Gregarina termitis* Leidy*Termes flavipes*; *T. lucifugus* Rossi.

Family GREGARINIDAE Labbé 1899: 9

Genus GREGARINA Dufour 1828: 366

? GREGARINA TERMITIS Leidy

[Figures 51 and 56]

1881	<i>Gregarina termitis</i>	Leidy	1881: 425
1897	<i>Gregarina termitis</i>	Porter	1897: 65
1899	<i>Gregarina termitis</i>	Labbé	1899: 36
1903	<i>Gregarina termitis</i>	Crawley	1903: 44
1903	" <i>Gregarina</i> " <i>termitis</i>	Minchin	1903: 337
1913	<i>Gregarina termitis</i>	Ellis	1913: 289

Sporonts solitary, obese ovoidal. Length 60μ , width 36μ . Ratio LP : TL :: 1 : 3.3 WP : WD :: 1 : 1.2. Protomerite dome-shaped, twice as wide as high, deep constriction at septum. Deutomerite ovoidal, tapering to a rather sharp point. Nucleus spherical, one karyosome.

Epimerite and cysts unknown.

Intestine of *Termes flavipes*; *T. lucifugus* Rossi.

Taken at Philadelphia, Pa., Cambridge, Mass., and Boulder, Colo.

Leidy found but one gregarine in his host, but Porter reports the parasites "very common in some hosts," in the anterior part of the small intestine only. Porter illustrates a section of the intestine in which are "great numbers of cysts." The sections, however, are undoubtedly those of adult sporonts cut crosswise and obliquely, with dark-staining nuclei often sectioned, as often not. A figure (Fig. 74, Pl. VI, of Porter) showing an adult solitary sporont in which the protoplasmic granules are fairly large and regularly spherical is described as "that of one filled with sporocysts." Porter's figure of a sporont is almost identical with that of Leidy (Plate 52, fig. 27).

Crawley opened "perhaps a dozen termites" in search for the parasite but did not encounter it.

I have examined many termites at different seasons. They were abundantly parasitised with Infusoria (Leidy 1881, and Kofoid and Swezey 1919) but no gregarines were recovered.

Ellis described the species from western termites. His drawing (my figure 56) compares favorably with that of Leidy except that the posterior end of his is broadly rounded instead of bluntly pointed. The newer specimens are also much larger—570 μ long. Dimensions given by Ellis are "P. 25 μ x 170 μ , D. 30 μ x 400 μ ." They correspond with his figure (Pl. XVII, fig. 6) if changed to "P. 250 μ by 170 μ , D. 300 μ by 400 μ ."

This species is considered doubtful because three important characters are lacking, viz. epimerite, cyst and spores. None of the workers has encountered associations.

LIST OF SPECIES FOUND IN THE ORDER HEMIPTERA OF
THE CLASS HEXAPODA

PARASITE	Host
ACTINOCEPHALIDAE	
<i>Coleorhynchus heros</i> (Schneider) Labbé	<i>Nepa cinerea</i> L.
UNCERTAIN SPECIES	
[? <i>reduvii</i> Ramdohr]	<i>Reduvius personatus</i> (L.)
MISCELLANEOUS	
[no name]	<i>Phymata crassipes</i>

Family ACTINOCEPHALIDAE Léger 1892: 166

Genus COLEORHYNCHUS Schneider 1885: 94, emend.
Labbé 1899: 23

Epimerite unknown. Protomerite a rounded shallow disc depressed centrally with a cape overlapping the deutomerite. Septum convex upward. Simple rupture of cysts, spores biconical.

COLEORHYNCHUS HEROS (Schneider) Labbé Type Species

[Figures 48 and 49]

1885	<i>Coleophora heros</i>	Schneider	1885: 95
1899	<i>Coleorhynchus heros</i>	Labbé	1899: 23
1903	<i>Coleorhynchus heros</i>	Minchin	1903: 200, 335
1913	<i>Coleorhynchus heros</i>	Ellis	1913: 276

Sporonts solitary, length 2 to 3 mm. Width not given. Ratio LP : TL :: 1 : 4; WP : WD :: 1 : 1. Protomerite a round flattened disc centrally depressed, border slightly irregular with a cape extending down over the deutomerite. Septum convex upward. Deutomerite ovoidal, blunt at posterior end. Epimerite and nucleus not known.

Cyst dehiscence by simple rupture, spores sharply biconical.

Taken at Poitiers, France.

Intestine of *Nepa cinerea* L.

Uncertain Species

[? *reduvii* Ramdohr]

[Figure 50]

1811	<i>Vibrio Reduwii</i>	Ramdohr	1811: 194
1848	<i>Sporadina Reduwii</i>	Stein	1848: 213, 223
1848	<i>Sporadina Reduwii</i>	Frantzius	1848: 195
1859	<i>Gregarina Reduwii</i>	Diesing	1859: 734
1863	<i>Gregarina Reduwii</i>	Lankester	1863: 94
1899	<i>Hyalospora reduvii</i>	Labbé	1899: 14
1903	<i>Hyalospora reduvii</i>	Minchin	1903: 336

Taken at Berlin.

Intestine of *Reduvius personatus* (L.).Ramdohr placed the species with the Infusoria, in the genus *Vibrio*.

Stein gives these dimensions:

Sie zeigten sehr verschiedene Grösse, die grössten waren etwa $\frac{1}{5}$ ''' lang und $\frac{1}{38}$ ''' breit

He also observed cysts in which two sporonts were united. Nine spore-ducts were seen, with spore extrusion in chains. The spores were

. . . kung spindelförmig oder fast eiförmig, $\frac{1}{250}$ ''' by $\frac{1}{570}$ '''.

His illustrations show them to be well-rounded at the ends.

The genus *Hyalospora*, in which the specimens recorded were placed by Labbé, is characterized in part by (a) sporonts in associations of two, (b) cysts with simple rupture, (c) spores fusiform, sharply pointed at the ends.

The species in question does not belong in this genus because (a) among the great numbers of parasites seen by Stein none is mentioned as found in association and his figure indicates a solitary individual, (b) cyst dehiscence is accomplished through spore-ducts (nine in the figure of Stein), and (c) with spores extruded in chains. The spores are ellipsoidal, rounded at the ends.

It is evident that the species belongs in the family Gregarinidae from the method of cyst dehiscence. I have placed it with the Uncertain Species because of insufficient data. It seems to most closely resemble the genus *Leidyana* Watson.

Miscellaneous

No Name

1828	<i>Gregarina Phymatae crassipedis</i>	Dufour	1828: 206
1837	<i>Gregarina soror</i>	Dufour	1837: 12
1846	<i>Gregarina soror</i>	Frantzius	1846: 11, 28
1851	<i>Gregarina soror</i>	Diesing	1851: 11
1863	<i>Gregarina soror</i>	Lankester	1863: 94
1903	<i>Gregarina soror</i>	Minchin	1903: 336

Dufour says concerning this animal life:

Subsphericum alba, cephalothorace abdominis dimidiam partem adaequante.

From the figure and description of Dufour it is obvious that what he observed were not sporonts but cysts. There is no record of sporonts being found, and the error was a very natural one at the time.

LIST OF SPECIES FOUND IN THE ORDER NEUROPTERA OF
THE CLASS HEXAPODA

PARASITE	HOST
GREGARINIDAE	
<i>Gregarina clavata</i> Kölliker	<i>Ephemera vulgata</i> larv.
<i>Gregarina mystacidarum</i> Frantzius	<i>Mystacides</i> sp., larv.
<i>Gregarina marteli</i> Léger	<i>Embia Solieri</i> Ramb., larv.
<i>Gamocys is ephemeræ</i> (Frantzius) Labbé	<i>Ephemera vulgata</i> , larv.
	<i>Ephemera</i> sp., larv.
ACTINOCEPHALIDAE	
<i>Actinocephalus sieboldii</i> (Kölliker) Frantzius	<i>Agrion</i> sp., larv.
<i>Actinocephalus octacanthus</i> Frantzius	<i>Phryganea</i> sp.
<i>Actinocephalus brachydactylus</i> Ellis	<i>Aeschna</i> sp.
<i>Geneiorhynchus monnieri</i> Schneider	<i>Libellules</i> sp.
Type species	
<i>Genriorhynchus aeschnæ</i> Crawley	<i>Aeschna constricta</i> Say.
<i>Bothriopsis claviformis</i> Pinto	<i>Aeschnida</i> sp., larv.
<i>Asterophora mucronata</i> Léger	<i>Rhyacophila</i> sp.
Type species	
<i>Asterophora elegans</i> Léger	<i>Phryganea grandis</i> , larv.
	<i>Sericostoma</i> sp., larv.
<i>Discorhynchus truncatus</i> (Léger) Labbé	<i>Sericostoma</i> sp. larv.
Type species	
<i>Pileocephalus chinensis</i> Schneider	<i>Mystacides</i> sp., larv.
Type species	
<i>Pileocephalus heerii</i> (Kölliker) Schneider	<i>Phryganea varia</i> (Fab.) larv.
<i>Hoplorhynchus oligacanthus</i> (von Siebold)	<i>Calopteryx virgo</i> L., larv.
Schneider	<i>C. splendens</i> Harb. larv.
Type species	
ACANTHOSPORIDAE	
<i>Ancyrophora uncinata</i> Léger	<i>Sericostoma</i> sp., larv.
	<i>Phryganea rhumbica</i> , larv.
	<i>Dytiscus</i> sp., larv.
	<i>Colymbetes</i> sp., larv.
	<i>Limnophilus rhombicus</i> , larv.
<i>Prismatospora evansi</i> Ellis	<i>Tramea lacerata</i> Hagen
Type species	<i>Sympetrum rubicundulum</i> Say
MENOSPORIDAE	
<i>Menospora polyacantha</i> Léger	Type species
	<i>Agrion puella</i> , larv.
SPECIES OF DOUBTFUL POSITION	
[? <i>psocorum</i> von Siebold]	<i>Psocus</i> sp.

Family GREGARINIDAE Labbé 1899: 9

Genus GREGARINA Dufour 1828: 366

GREGARINA CLAVATA Kölliker

[Figures 22 and 89]

1848	<i>Gregarina clavata</i>	Kölliker	1848: 10
1848	<i>Gregarina clavata</i>	Frantzius	1848: 194
1848	<i>Sporadina clavata</i>	Frantzius	1848: 195
1851	<i>Gregarina clavata</i>	Diesing	1851: 14
1859	<i>Gregarina clavata</i>	Diesing	1859: 734
1863	<i>Gregarina clavata</i>	Lankester	1863: 94
1863	<i>Zygocystis clavata</i>	Lankester	1863: 94
1887	<i>Clepsidrina granulosa</i>	Schneider	1887: 74, 77, 78
1899	<i>Gregarina granulosa</i>	Labbé	1899: 11
1903	<i>Gregarina granulosa</i>	Minchin	1903: 334
1911	<i>Gregarina granulosa</i>	Wellmer	1911: 119

Of the original observation by Kölliker only a single immature specimen is illustrated which furnishes a clue to the identity of the parasite. The sporont is short and stout, 30 by 16μ , the ratio of LP : TL :: 1 : 2.5; WP : WD :: 1 : 1. The protomerite is dome-shaped with a small apical cone and a deep constriction at the septum. The deutomerite is ovoidal and the nucleus spherical with one karyosome.

Intestine of *Ephemera vulgata*, larva.

Taken at Zürich, Poitiers, France, and in East Prussia.

Kölliker records that Frantzius had found this species (1845) but Frantzius' drawings (1848, Pl. VII, figs. VII, 1, 2, 3, and 4) are very unlike the figure of Kölliker (Fig. 89, this paper) and represent clearly the species *Gamocystis ephemerae*.

Diesing (1859) records:

Receptaculum subhemisphaericum apiculo terminali conico. Corpus longe ovatum, lacteum. Longit. $1/26'''$; crassit. $1/69'''$.

Schneider (p. 74) reports finding *Gamocystis ephemerae* and also another gregarine:

Le Grégarine qui domine qu'on trouve toujours dans ces larves, est la curieux *Gamocystis Francisci*. Beaucoup plus rare et toujours en petit nombre est au contraire la Grégarine actuelle, qui se fait en revanche remarquer par une belle taille (518 μ le primite).

It is characterized by the very large granules in the endocyte of the protomerite. Chromidial inclusions in the deutomerite. Ratio LP ; TL :: 1 : 5 (Primite) to 1 : 9 (Satellite). WP : WD :: 1 : 1.5. The nucleus is spherical, 51μ in diameter with one karyosome 26μ in diam. The sporont is cylindrical, the protomerite dome-shaped with a deep constriction at the septum. The deutomerite is cylindrical with a shoulder and truncate at the free end.

While the observations of the two authors are not comparable, the first from an immature specimen only, yet there is a probability of their being identical, the hosts being the same. In order therefore to reduce the number of older incompletely described species they should be absorbed wherever possible. In the present species there are at least no conflicting characters.

GREGARINA MYSTACIDARUM Frantzius

[Figure 76]

1848	<i>Gregarina Mystacidarum</i>	Frantzius	1848: 193, 196
1848	<i>Gregarina Mystacidarum</i>	Stein	1848: 188
1851	<i>Gregarina Mystacidarum</i>	Diesing	1851: 12
1859	<i>Gregarina Mystacidarum</i>	Diesing	1859: 734
1863	<i>Gregarina Mystacidarum</i>	Lankester	1863: 94
1875	<i>Clepsidrina mystacidarum</i>	Schneider	1875: 592
1899	<i>Gregarina mystacidarum</i>	Labbé	1899: 11
1903	<i>Gregarina mystacidarum</i>	Minchin	1903: 335
1911	<i>Gregarina mystacidarum</i>	Wellmer	1911: 118

Sporonts in pairs, long-cylindrical, Ratio LP:TL :: 1:6 to 10; WP:WD :: 1:1. Protomerite cylindrical, truncate at free end, slightly constricted at septum. Deutomerite cylindrical, broadly rounded posteriorly. Nucleus spherical. Epimerite not known. Cysts spherical.

Taken at Berlin and in East Prussia. Host *Mystacides* sp., larva.

This host is also parasitized by *Pileopcehalus chinensis* Schn.

GREGARINA MARTELI Léger

[Figures 36 and 37]

1904	<i>Gregarina Marteli</i>	Léger	1904: 358
1911	<i>Gregarina Marteli</i>	Sokolow	1911: 279

Sporonts in pairs, elongate, slender. Length 100 to 150 μ . Width not given. Ratio LP:TL :: 1:10; WP:WD :: 1:1. Protomerite of primitive conoidal, blunt at apex and dilated in posterior two-thirds. Protomerite, of satellite deeply cupped in anterior portion. Constriction at septum. Deutomerite elongate-cylindrical, of same width throughout, ending in a broad blunt extremity. Epimerite a simple globular papilla. Nucleus spherical. Cyst and spores unknown.

Host: *Embia Solieri* Ramb., larv. Intestine.

Taken at Cavaliere, France.

This host is also parasitized with *Diplocystis clerici* Léger (Monocystid Gregarine) and *Adela transita* Léger (Coccidian).

Genus GAMOCYSTIS Schneider 1875: 586; 1882: 443

Sporonts biassociative, united in apposition, ovoidal, stout-bodied, resembling a Monocystid. Protomerite only in trophozoite. Sporulation partial. Cyst without spore-ducts. Spores elongate-cylindrical.

GAMOCYSTIS EPHEMERAE (Frantzius) Labbé

[Figures 38 and 90]

1843	<i>Zygocystis Ephemeræ</i>	Frantzius	1843: 194
1848	<i>Gregarina clavata</i>	Kölliker	1848: 10
1848	<i>Zygocystis Ephemeræ</i>	Frantzius	1848: 194
1851	<i>Gregarina clavata</i>	Diesing	1851: 553
1859	<i>Gregarina Ephemeræ</i>	Diesing	1859: 736
1882	<i>Gamocystis Francisci</i>	Schneider	1882: 444
1887	<i>Gamocystis Francisci</i>	Schneider	1887: 74
1899	<i>Gamocystis ephemeræ</i>	Labbé	1899: 12
1903	<i>Gamocystis ephemeræ</i>	Minchin	1903: 197, 334

Sporonts in pairs, in apposition. No protomerite. Body broadly ovoidal, truncate at apices, flattened at place of union. Length of primate 110μ , of satellite 130μ . Width of former 80μ , of latter same. Sarcocyte thickened at the two apices. Endocyte dense, with large irregular granules. Nucleus spherical, 30μ , one karyosome. Cyst and spores not known.

Intestine of *Ephemeræ* sp., larva, *Ephemeræ vulgata*, larva.

Taken at Zürich and in Indre-et-Loire, France.

There seems to be no doubt that the species seen by Frantzius and by Schneider are identical from a comparison of the figures given by each. The ratio of length to width in the figures of Frantzius is about two to one, in the figure of Schneider one and one-half to one.

Labbé considers Kölliker's *Gregarina clavata* identical with the above species, probably because of a similarity of the host. The species are, however, quite different.

Minchin considers the present species identical with *Gamocystis francisci* Schn.

Schneider (1882: 445) offers this phylogenetic hypothesis: The genus *Ephemeræ* has been considered a pseudo-neuropteran closely allied to the Orthoptera, in which group the only other species of the genus *Gamocystis* has been found.

Family ACTINOCEPHALIDAE Léger 1892: 166

Genus ACTINOCEPHALUS Stein 1848: 196

Epimerite small, sessile or upon a short neck, with 8 to 10 short sharp spines or simple bifurcate digitiform processes. Spores biconical.

ACTINOCEPHALUS SIEBOLDII (Kölliker) Frantzius

[Figure 12]

1839	?	von Siebold	1839: 67
1848	<i>Gregarina Sieboldii</i>	Kölliker	1848: 10
1848	<i>Actinocephalus Sieboldii</i>	Frantzius	1848: 195
1851	<i>Gregarina Sieboldii</i>	Diesing	1851: 7
1859	<i>Gregarina Sieboldii</i>	Diesing	1859: 731
1863	<i>Gregarina oligacantha</i>	Lankester	1863: 94
1899	<i>Hoplorhynchus oligacanthus</i>	Labbé	1899: 30

Sporonts solitary, rather obese. Total length '0.162 to 0.188''' (Kölliker), Width 0.045'''. Ratio LP:TL :: 1:4 to 5; WP:WD :: 1.3:1. Protomerite rounded, slightly wider than high, constriction at septum. Deutomerite narrower than protomerite, tapering to a blunt posterior extremity. Epimerite composed of 4 to 6 sharp recurved hooks set upon a long cylindrical neck. Nucleus spherical with one or two large karyosomes.

Host: Larva of several species of Agrion. Intestine.

Taken at Danzig, Wurtzburg.

Kölliker says this species was first taken by von Siebold but not described. Kölliker described it in detail and assigned to it a name.

Frantzius placed it in the genus *Actinocephalus* because of the character of the epimerite.

Labbé placed the species with *Hoplorhynchus oligacanthus* Schn. because of a close similarity with this genus. While the epimerites of the two species are similar, Kölliker's species having 4 to 6 recurved hooks and Schneider's 6 to 8, the hooks on the former species are sharply pointed and decidedly recurved while those on the latter number eight as a maximum and are but slightly recurved and blunt at the tips. (Cf. Figs. 13 and 14 (*Hoplorhynchus oligacanthus*) with Fig. 12, the present species).

The writer has differentiated the two species on this point and a dissimilarity of the nuclei. Schneider's new genus, *Hoplorhynchus*, is characterized by an elongate-ovoidal nucleus while the nucleus in Kölliker's species is spherical.

ACTINOCEPHALUS OCTACANTHUS Frantzius

[Figure 74]

1848	<i>Gregarina Heerii</i>	Frantzius	1848: 193
1848	<i>Actinocephalus octacanthus</i>	Frantzius	1848: 192, 194, 195
1851	<i>Gregarina Heerii</i>	Diesing	1851: 552
1851	<i>Gregarina Frantziusiana</i>	Diesing	1851: 8
1863	<i>Gregarina Heerii</i>	Lankester	1863: 94

Host: *Phryganea* sp. Intestine.

Frantzius recognized that this species was different from the *Gregarina Heerii* of Kölliker from the same host, and illustrates epimerites of the two species, but his drawings are confusing for in another place he calls the same drawing now one name, now the other.

Diesing regarded the two species as synonymous on one page (552) and still separates them on another, creating a new species for the present species, *Gregarina frantziusiana*. He differentiates the two thus:

Gregarina frantziusiana Diesing:

Proboscis globosa, uncinulorum, octo coronula terminali simplici (octolobia Frantzius).
 Corpus subellipticum turgidum

Gregarina heerii Kölliker.

Proboscis antrorsum obovato-lanceolata, granulis exasperata, retrorsum subelliptica laevis,
 inermis? Corpus longe ovatum

Hab. *Phryganea grandis* larva, intestine, in both.

From then on the present species is lost in the species *Pileocephalus heerii*. It is obvious from a comparison of the epimerites that two very different species have been confused and that the original designation of Frantzius still holds.

ACTINOCEPHALUS BRACHYDACTYLUS Ellis

[Figures 44 and 45]

1913 *Actinocephalus brachydactylus* Ellis 1913: 279, 289

Sporonts solitary, elongate-ovoidal. Length 501 μ . Ratio LP: :1:3 to 4;
 WP:WD: :1:1. Protomerite well-rounded, with same width as height,
 slight constriction at septum. Deutomerite slightly wider at shoulder,
 tapering gently and ending in a blunt point. Epimerite very short, a
 corona of eight short digitiform processes.

Cyst and spores unknown.

Habitat not given. Host: Nymphs of *Aeschna* sp.

Taken at Douglas Lake, Michigan.

Genus GENEIORHYNCHUS Schneider 1875: 594

Epimerite a tuft of short bristles set at the apex of a long slender neck.
 Spores cylindro-biconical.

GENRIORHYNCHUS MONNIERI Schneider Type species

[Figures 19, 20, and 21]

1875	<i>Geneiorhynchus Monnieri</i>	Schneider	1875: 595
1899	<i>Geneiorhynchus monnieri</i>	Labbé	1899: 25
1903	<i>Geneiorhynchus monnieri</i>	Minchin	1903: 200, 335
1913	<i>Geneiorhynchus monnieri</i>	Ellis	1913: 274

Sporonts solitary, obese, ovoidal. No dimensions given. Ratio
 LP:TL: :1:4; WP:WD: :1:1.3. Protomerite very broadly rounded,
 acuminate at apex. Slight constriction at septum. Deutomerite widest
 at mid-portion, ending in an acute point. Epimerite a tuft of short sharp
 bristles set at apex of a long slender neck. Nucleus spherical with several
 karyosomes. Cyst dehiscence by simple rupture, spores sub-navicular.

Intestine of *Libellules* sp.

Taken near Paris.

GENEIORHYNCHUS AESCHNAE Crawley

[Figure 40]

1907	<i>Geneiorhynchus aeshnae</i>	Crawley	1907: 227
1911	<i>Geneiorhynchus aeshnae</i>	Sokolow	1911: 282
1913	<i>Geneiorhynchus aeshnae</i>	Ellis	1913: 275, 289

Sporonts solitary, cylindrical. Length of trophozoite 420μ . Ratio (without epimerite) LP:TL: :1:3. WP:WD: :1.1:1 Protomerite widest at base, curving gently anteriorly, ending in a truncate cone. No constriction at septum. Deutomerite narrower than protomerite at septum, tapering thence and ending in a broad truncated extremity. Epimerite a large globular papilla borne on a short stout neck from the protomerite and "liberally provided with short spines directed backward." (Crawley). Nucleus spherical with several karyosomes. Sarcocyte in apex of protomerite very thick. Endocyte not dense, nucleus visible in vivo. Cyst and spores not known.

Intestine? of *Aeschna coustricta* Say. (*Aeschna c.*)

Taken in Southeastern Pennsylvania.

Genus BOTHRIOPSIS Schneider 1875: 596

Epimerite an ovoidal structure with six or more long slender filaments. Protomerite very large, septum convex upward. Spores biconical.

BOTHRIOPSIS CLAVIFORMIS Pinto

[Figure 61]

1918	<i>Bothriopsis claviformis</i>	Pinto	1918: ?
1919	<i>Bothriopsis claviformis</i>	Pinto	1919: 87

Sporonts elongate-triangular, widest at anterior end, bluntly acuminate posteriorly. Dimensions: 100 to 200μ in length, 70 in width (of protomerite). Ratio LP:TL: :1:7; WP:WD: :1.4 : 1. Nucleus spherical to irregular in shape.

Intestine of *Aeschnida* sp.

Taken at Manguinhos, Brazil.

Genus ASTEROPHORA Léger 1892: 129

Epimerite a thick long disc with a milled border and a long stout style projecting upward from the center. Spores cylindro-conical.

ASTEROPHORA MUCRONATA Léger Type species

[Figures 25 and 26]

1892	<i>Asterophora mucronata</i>	Léger	1892: 130
1899	<i>Asterophora mucronata</i>	Labbé	1899: 22
1903	<i>Asterophora mucronata</i>	Minchin	1903: 200, 336

Sporonts solitary, elongate-ovoidal. Length 350μ , width not given. Ratio LP:TL: :1:2.2. WP:WD: :1:1.1. Protomerite elongate (twice as

long as wide), tapering upward from septum to a blunt conoidal anterior end. Deep constriction at septum. Deutomerite of same shape as protomerite and but little longer. Epimerite a flat disc with milled border and long blunt central style set upon a fairly stout neck. Nucleus ovoidal with several karyosomes. Cysts spherical, 150–200 μ . Dehiscence by simple rupture. Spores cylindro-biconical, 8 by 3.5 μ .

Host: Larva of *Rhyacophila* sp. Intestine.

Taken in the Valley of the Loire, France.

ASTEROPHORA ELEGANS Léger

[Figures 23, 24, and 43]

1892	<i>Asterophora elegans</i>	Léger	1892: 131
1899	<i>Asterophora elegans</i>	Labbé	1899: 22
1903	<i>Asterophora elegans</i>	Minchin	1903: 200,336

Sporonts solitary, elongate ovoidal. Length 450 μ . Width not given. Ratio LP:TL: :1:3; WP:WD: :1:1.1. Protomerite very elongate (almost twice as long as wide), tapering regularly upward from septum to a long blunt anterior end. Deep constriction at septum. Deutomerite of same shape as protomerite but twice as long. Epimerite a flat disc with a milled border and a short central style set upon a fairly stout neck which is of the same length as the protomerite. Nucleus slightly ovoidal with several karyosomes.

Cysts spherical, 300 to 400 μ . Spores biconical, much larger than in *Asterophora mucronata*, 12.7 by 4.25 μ .

Intestine of *Phryganea grandis*, larva, *Sericostoma* sp., larva.

The former host is also parasitized with *Pileocephalus heerii*, the two parasites generally found together. *Sericostoma* is also parasitized with *Discorhynchus truncatus*.

Genus DISCORHYNCHUS Léger 1892: 134; Labbé 1899: 20

Epimerite a short-stalked, large flattened globular structure with a still larger horizontal collar around its base. Spores biconical.

DISCORHYNCHUS TRUNCATUS (Léger) Labbé Type species

[Figures 28 and 29]

1892	<i>Discorhynchus truncatus</i>	Léger	1892: 134
1899	<i>Discorhynchus truncatus</i>	Labbé	1899: 20
1903	<i>Discorhynchus truncatus</i>	Minchin	1903: 199, 337
1913	<i>Discorhynchus truncatus</i>	Ellis	1913: 275

Sporonts solitary, almost rectangular. Length 300μ , width not given. Ratio LP:TL: :1:4; WP:WD: :1.2 : 1. Protomerite irregularly rounded, bluntly conoidal at apex, widest at mid-portion. Constriction at septum. Protomerite wider than deutomerite. Deutomerite rectangular, in optical section, flat at base. Epimerite a short stout neck with a large flattened papilla at apex. Around the base of the papilla fits a much larger flattened disc like a collar. Nucleus spherical, with several karyosomes.

Cysts spherical, 140μ . Spores biconical, slightly crescentic.

Taken in Poitou, France.

Intestine of a neuropteran doubtfully identified as the larva of *Sericostoma* sp.

Genus PILEOCEPHALUS Schneider 1875:591

Epimerite a small lance-shaped or simple conoidal papilla placed unstalked upon the protomerite. Spores biconical.

PILEOCEPHALUS CHINENSIS Schneider Type species

[Figures 17, 18, 93, and 94]

1875	<i>Pileocephalus chinensis</i>	Schneider	1875: 592
1885	<i>Pileocephalus chinensis</i>	Schneider	1885: 10
1899	<i>Pileocephalus chinensis</i>	Labbé	1899: 19
1903	<i>Pileocephalus chinensis</i>	Minchin	1903: 199, 335
1911	<i>Pileocephalus chinensis</i>	Wellmer	1911: 128
1913	<i>Pileocephalus chinensis</i>	Ellis	1913: 274

Sporonts solitary, stout bodied, ovoidal. Measurements not given; “. . . toujours de taille assez petite . . . ” Ratio LP:TL: :1:5; WP:WD: :1:1. Protomerite broadly rounded, apex pointed, slightly wider than high. Constriction at septum. Deutomerite widest at shoulder, tapering from thence and ending in a broad blunt extremity. Epimerite a small unstalked papilla, conoidal at apex. Nucleus spherical.

Cysts spherical, spores roughly triangular with long slender ends. (Figs. 93, 94.)

Taken near Paris.

Intestine of *Mystacides* sp., larva.

This species received its name from the character of the epimerite concerning which Schneider says:

Epimérite triangulaire ou cordiforme en manière de bonnet chinois

The insect is also the host of *Gregarina mystacidarum* Frantzius, and Schneider and Wellmer found associations of the parasite in the host with the above described species.

PILEOCEPHALUS HEERII (Kölliker) Schneider
[Figures 15, 16, 46, 72 and 73]

1845	<i>Gregarina Heerii</i>	Kölliker	1845: 100
1848	<i>Gregarina Heerii</i>	Kölliker	1848: 6
1848	<i>Gregarina Heerii</i>	Frantzius	1848: 193
1848	<i>Stylorhynchus Heerii</i>	Frantzius	1848: 195
1851	<i>Gregarina Heerii</i>	Diesing	1851: 552
1851	<i>Gregarina Frantziusiana</i>	Diesing	1851: 8
1859	<i>Gregarina Heerii</i>	Diesing	1859: 728
1859	<i>Gregarina Frantziusiana</i>	Diesing	1859: 730
1863	<i>Stylorhynchus Heerii</i>	Carus	1863: 570
1863	<i>Gregarina Heerii</i>	Lankester	1863: 95
1887	<i>Pileocephalus Heerii</i>	Schneider	1887: 199
1899	<i>Pileocephalus heerii</i>	Labbé	1899: 19
1903	<i>Pileocephalus heerii</i>	Minchin	1903: 199, 336

Sporonts solitary, capable of great contractility due to unusually well-developed myonemes. Trophozoite when quiescent long and arrow-shaped, widest in middle and tapering in both directions, sharply acuminate at extremities (Fig. 15). In sporonts the same general shape but much contracted longitudinally and proportionally broader. (Fig. 16). Dimensions not given. Ratio LP:TL: : (quiet trophozoite without epimerite) 1:3 (contracted sporont 1:2). WP:WD: :1:1. Protomerite widest just above septum, conical, apex truncate. Deep constriction at septum. Deutomerite same shape, ending acuminately. Nucleus ellipsoidal with many small karyosomes. Epimerite highly specialized. In young trophozoites an elongate papilla sharply acuminate and situated upon a short neck. In older specimens there develops a spade-shaped or lanceolate (in optical section) holdfast, at the end of a bulbous neck (the former papilla). The neck and lance are of equal length and surmount the truncate protomerite. The trophozoite in this form is a very beautiful animal (Fig. 15).

Spores from cysts in feces biconical, which is the accepted form for the type, as mentioned in the genus synopsis.

A possible schizogony exists, for in this species cysts were encountered in the coelom which developed triangular spores. Schneider attributes these latter spores to the species in question but he suggests that they may belong to another parasite. If the discovery is authentic, the fact adds one link in the hypothesis of Minchin that the Cephaline Gregarines are capable of schizogony as well as sporogony. If this should be proven an impossibility, then the present species must be removed from the Eugregarinae and placed with the Schizogregarinae.

Schneider found only triangular spores in the type species *P. chinensis*, but does not state whether they emanated from coelomic or fecal cysts, mentioning only the latter type of cysts.

Habitat: Intestine of *Phryganea varia* (Fabricius), larva.

Taken at Wurzburg, and Poitiers (France).

Kölliker gives as hosts *Phryganea grandis* 'and other Phryganeidae larvae.' The only point of serious conflict between the two sets of observations lies in the shape of the nucleus. We are led to believe this one of the fixed characters of a species, but Kölliker finds the nucleus to be spherical, while Schneider says it is ovoidal. In *P. chinensis*, however, it is spherical, so this is not a genus character.

Schneider does not doubt the identity of the two species.

La figure donnee par Kölliker ne laisse aucun doute sur la synonymie,

Frantzius gives a beautiful figure of a trophozoite which agrees in every particular with the observations of others except that the nucleus here too is spherical (Fig. 72, this paper). I am inclined to think Schneider's observations were in error or mis-interpreted in the rapidly moving animals and that the correct shape in all three sets of data is spherical.

Genus HOPLORHYNCHUS Carus 1863:570

Sporonts slender with elongate ovoidal nuclei. Epimerite a very long neck with six to eight slightly recurved hooks. Cyst dehiscence by simple rupture. Spores ellipsoidal.

HOPLORHYNCHUS OLIGACANTHUS (von Siebold) Schneider

Type species

[Figures 13 and 14]

1839	<i>Gregarina oligacanthus</i>	von Siebold	1839: 67
1845	<i>Gregarina oligacantha</i>	Dujardin	1845: 638
1845	<i>Gregarina oligacantha</i>	Kölliker	1845: ?
1848	<i>Gregarina oligacantha</i>	Kölliker	1848: 10
1848	<i>Stylorhynchus oligacanthus</i>	Stein	1848: 195, 222
1848	<i>Stylorhynchus oligacanthus</i>	Frantzius	1848: 195
1851	<i>Gregarina oligacantha</i>	Diesing	1851: 7
1859	<i>Gregarina oligacantha</i>	Diesing	1859: 730-1
1863	<i>Gregarina oligacantha</i>	Lankester	1863: 95
1875	<i>Hoplorhynchus oligacanthus</i>	Schneider	1875: 591
1899	<i>Hoplorhynchus oligacanthus</i>	Labbé	1899: 30
1903	<i>Hoplorhynchus oligacanthus</i>	Minchin	1903: 201, 333
1911	<i>Hoplorhynchus oligacanthus</i>	Wellmer	1911: 139
1913	<i>Hoplorhynchus oligacanthus</i>	Ellis	1913: 275

Sporonts solitary, slender. Dimensions not given. Ratio LP:TL: : 1:4; WP:WD: :1:1. Protomerite irregularly rounded, slightly wider than deutomerite. Widest at mid-region, constricted at septum. Deutomerite irregularly cylindrical, tapering posteriorly and ending in a blunt point. Epimerite a corona of six to eight slightly recurved hooks set upon a long

slender cylindrical neck. Nucleus elongate-cylindrical with many small karyosomes.

Cyst and spores as in genus characters.

Intestine of *Calopteryx* (*Callopteryx*, Schneider) *virgo* L., larva, and *C. splendens* Harb. larva.

Taken at Danzig, Berlin and Paris.

With all the authors who mention the species, only one gives adequate figures, Schneider, from whom the data and drawings is taken.

Diesing (1859) reports:

Proboscis longissima gracilis medio ventricosa, apice subglobosa, spinularum (circa 9) corona simplici. Receptaculum subglobosum compressum. Corpus conicum lacteum receptaculo quinque longius.

Lankester considers *Actinocephalus sieboldii* and the present species synonymous.

Family ACANTHOSPORIDAE, Léger 1892: 167

Sporonts solitary, epimerite simple or appendicular. Dehiscence by simple rupture. Spores with equatorial and polar spines.

Genus ANCYROPHORA Léger 1892: 146

Epimerite a globe with a corona of not more than 12 backwardly-directed blunt hooks. Spores biconical with equatorial and polar spines.

ANCYROPHORA UNCINATA Léger

[Figures 27, 41 and 42]

1848	<i>Gregarina Dytiscorum</i>	Frantzius	1848: 194
1892	<i>Ancyrophora uncinata</i>	Léger	1892: 147
1899	<i>Ancyrophora uncinata</i>	Labbé	1899: 28
1903	<i>Ancyrophora uncinata</i>	Minchin	1903: 201, 335
1916	<i>Ancyrophora uncinata</i>	Watson	1916a: 164

Sporonts solitary, elongate. Length 150–200 μ . Protomerite well rounded, deeply constricted at septum. Deutomerite widest at shoulder, tapering from thence to a long slender acuminate posterior extremity. Epimerite a corona of twelve or less short blunt recurved hooks, superimposed upon a distinct but rather short stout neck. The hooks are arranged in two levels, the upper group being larger and stouter. Nucleus spherical with several karyosomes.

Cysts spherical, 200 μ , spores biconical, hexagonal in optical section, with four spines at each pole and six on equator. Spores 8 by 6 μ .

Intestine of larvae of *Sericostoma* sp., *Phryganea rhumbica*, and of two beetles, *Dytiscus* sp. and *Colymbetes* sp. Minchin adds *Limnophilus rhombicus*, probably a synonym of the second.

Taken in France.

The fact that this species is found in such widely varying hosts is unusual but not unique in the history of gregarines.

Genus PRISMATOSPORA Ellis 1914: 215

Spores hexagonal, truncate at ends with one row of long spines at each pole. Epimerite subglobose with lateral recurved hooks.

PRISMATOSPORA EVANSI Ellis Type species

[Figures 95, 96, 97, and 99]

1914 *Prismatospora evansi* Ellis 1914: 215

Sporonts broadly conical 400μ in average length. Ratio LP:TL: :1:3; WP:WD: :1:1. Protomerite broad, blunt, deutomerite tapering. Nucleus small, spherical.

Cysts subspherical, 370μ in diameter. Dehiscence by simple rupture. Spores as in genus, six long spines encircling each pole a short distance from the end, 11 by 5.8μ .

Intestine of *Tramea lacerata* Hagen. and *Sympetrum rubicundulum* Say.

Taken at Douglas Lake, Michigan.

The sporonts of this species are peculiar in that the protomerite is drawn out into digitiform processes at the apex in vivo, which may aid the animal in retaining its hold upon the intestine in so active a host where abdominal contractions might thrust it from the canal. These processes disappear when the animal is placed in water.

Family MENOSPORIDAE Léger 1892:168

Sporonts solitary. Epimerite a large cup bordered with hooks and placed on a long slender collar. Cyst dehiscence by simple rupture. Spores crescentic, smooth.

Genus MENOSPORA Léger 1892:151, 168

Characters of the family.

MENOSPORA POLYACANTHA Léger Type species

[Figures 30, 31 and 32]

1892 *Menospora polyacantha* Léger 1892: 151

1899 *Menospora polyacantha* Labbé 1899: 30

1903 *Menospora polyacantha* Minchin 1903: 201, 332

1913 *Menospora polyacantha* Ellis 1913: 275

Sporonts ovoidal, lanceolate, $600-700\mu$ in length. Width not given. Ratio LP:TL: : (trophozoite, without epimerite) 1:5; WP:WD: :1:1.1. Protomerite well rounded, deeply constricted at septum. Deutomerite widest just below septum, tapering gradually to a long sharply pointed

extremity. Epimerite a deep urn bordered with many short recurved hooks, superimposed upon a long slender neck two-thirds as long as the whole animal. Nucleus elongate-ovoidal, with one dumb-bell shaped karyosome.

Cysts spherical, 200 μ , spores smooth crescents 15 by 4 μ .

Taken in Poitou, France.

Intestine of *Agrion puella*, larva.

Species of Uncertain Position

[? psocorum von Siebold]

1839	<i>Gregarina Psocorum</i>	von Siebold	1839: 67
1846	<i>Gregarina Psocorum</i>	Frantzius	1846: 25
1848	<i>Gregarina Psocorum</i>	Frantzius	1848: 195
1851	<i>Gregarina ovata</i>	Diesing	1851: 10
1863	<i>Gregarina Psocorum</i>	Lankester	1863: 94
1911	<i>Hyalospora psocorum</i>	Wellmer	1911: 124

The only data outside the original reference, which is not available, are those of Diesing (1851):

Proboscis Receptaculum compressum. Corpus ovalum utrinque obtusum, receptaculo triplo longius. Longit. crassit . . .

Host: *Psocus* sp.

LIST OF SPECIES FOUND IN THE ORDER LEPIDOPTERA OF THE CLASS HEXAPODA

PARASITE	Host
GREGARINIDAE	
<i>Leidyana tinei</i> Keilin	<i>Endrosis fenestrella</i> Stain., larv.
UNNAMED SPECIES Keilin	<i>Oecophora pseudopretella</i> Stain., larv.
	<i>Tinea pallescentella</i> Stain., larv.

Family GREGARINIDAE Labbé 1899: 9

Genus LEIDYANA Watson 1915: 35

Sporonts solitary, epimerite a small sessile knob, dehiscence by spore-ducts. Spores in chains, barrel-shaped.

LEIDYANA TINEI Keilin

[Figures 115 and 116]

1918 *Leidyana tinei* Keilin 1918: 406

Sporonts solitary, long-ellipsoidal. Ratio LP:TL: :1: 7.5; WP:WD: : 1: 1.7. Maximum length 300 μ , width 85 μ . Protomerite hemispherical, deutomerite regularly ellipsoidal, tapering gently to a blunt posterior end.

Cysts spherical 110 μ in diameter. Spores barrel-shaped, 7 μ long.

Intestine of *Endrosis fenestrella* Stain.

Taken at Cambridge, England.

Unnamed Species Keilin

1918 Unnamed species Keilin 1918: 406
 Intestine of *Oecophora pseudospretella* Stain, and *Tinea pallescentella* Stain.

Taken at Cambridge, England.

“Very similar to species here described,” above, but a complete life-cycle was not procured, and the specimens left unnamed.

LIST OF SPECIES FOUND IN THE ORDER DIPTERA OF THE CLASS
 HEXAPODA

PARASITE	HOST
GREGARINIDAE	
<i>Gregarina longa</i> (Léger) Labbé	<i>Tipula</i> sp., larva
<i>Gregarina ctenocephalus</i> Ross	<i>Ctenocephalus serraticeps</i>
<i>Hirmocystis ventricosa</i> (Léger) Labbé	<i>Tipula oleracea</i> , larv.
Type species	
<i>Hirmocystis polymorpha</i> (Léger) Labbé	<i>Limnobia</i> sp., larv
	<i>Systemocerus caraboïdes</i> L., larv.
ACTINOCEPHALIDAE	
<i>Actinocephalus tipulae</i> (Hammerschmidt)	<i>Tipula oleracea</i> L., larv.
Léger	<i>Pachyrhina pratensis</i> L., larv.
<i>Actinocephalus</i> sp. Léger	<i>Ctenophora</i> sp., larv.
<i>Schneideria caudata</i> (von Siebold) Léger	<i>Sciara nitidicollis</i> Meig. larv.
<i>Schneideria mucronata</i> Léger Type species	<i>Bibio marci</i> (L.), larv.
<i>Schneideria</i> sp.	<i>Chironomus</i> sp., larv.
<i>Stylocystis praecox</i> Léger Type species	<i>Tanytus</i> sp., larv.
<i>Taeniocystis mira</i> Léger Type species	<i>Ceratopogon solstitialis</i> Winn., larv.
<i>Pileocephalus striatus</i> Léger and Duboscq	<i>Ptychoptera contaminata</i> , larv.

Family GREGARINIDAE Labbé 1899: 9

Genus GREGARINA Dufour 1828

GREGARINA LONGA (Léger) Labbé

[Figure 7]

1892	<i>Clepsidrina longa</i>	Léger	1892: 117
1899	<i>Gregarina longa</i>	Labbé	1899: 11
1903	<i>Gregarina longa</i>	Minchin	1903: 337
1911	<i>Gregarina longa</i>	Wellmer	1911: 114

Sporonts in pairs, very slender and elongate. Maximum length of sporont 500 μ . Width not given. Ratio LP:TL: :1:10 to 12; WP:WD: :1:1.2. Another form is found in which this ratio exists: LP:TL: :1:7, body less slender. Protomerite of primite well-rounded, deeply constricted at septum. Protomerite of satellite flattened at top, constricted in middle. Deutomerite regularly cylindrical, of approximately same width throughout in primite and tapering very slightly in satellite, ending in a broad blunt extremity. Epimerite a simple spherical papilla. Nucleus large, spherical, with one large karyosome.

Cysts spherical, 140 μ . Dehiscence by 7 or 8 short spore-ducts. Spores extruded in chains, dolioform, 6 by 5 μ .

Intestine of *Tipula* sp., larva.

Taken in the Valleys of the Vienne and Loire, France and in East Prussia.

GREGARINA CTENOCEPHALUS Ross

1909 *Gregarina ctenocephalus canis* Ross 1909: 359

1922 *Gregarina ctenocephalus* Kamm 1922 (this paper)

Sporonts spherical, no dimensions given. Epimerite pyriform, spores barrel-shaped. No dimensions given.

Intestine of *Ctenocephalus serraticeps*.

Taken at Port Said, Egypt.

Genus HIRMOCYSTIS Léger 1892: 110, emend. Labbé 1899: 12

Associations of from two to twelve sporonts. Epimerite small, cylindrical papilla. Cyst dehiscence by simple rupture. Spores ovoidal.

HIRMOCYSTIS VENTRICOSA (Léger) Labbé Type species [Figures 8 and 9]

1892 *Eirmocystis ventricosa* Léger 1892: 111

1899 *Hirmocystis ventricosa* Labbé 1899: 13

1900 *Eirmocystis ventricosa* Magalhães 1900: 39

1903 *Eirmocystis ventricosa* Minchin 1903: 336, 337

1911 *Hirmocystis ventricosa* Wellmer 1911: 123

1913 *Eirmocystis ventricosa* Ellis 1913: 264

Sporonts bi- or rarely tri- associative, obese. Length 180 μ , width not given. Ratio LP:TL: :1:3.5. WP:WD: :1:1.5 Protomerite broadly rounded in front, widest in the anterior half, much constricted and cylindrical in second half. No constriction at septum. Deutomerite broadens appreciably just below septum, widest in anterior third, tapering from thence, ending in a square extremity. Epimerite a small cylindro-conical papilla. Nucleus spherical, one karyosome.

Cysts spherical, 100 μ , dehiscence by simple rupture, spores ovoidal, not fusiform, 9 μ by 6 μ .

Intestine of *Tipula oleracea* and *Pachyrhina pratensis*, larvae.

Taken in the Valley of the Loire, France and in East Prussia.

Tipula sp. is also parasitized by *Gregarina longa* and *Actinocephalus tipulae*.

HIRMOCYSTIS POLYMORPHA (Léger) Labbé [Figures 10 and 11]

1892 *Eirmocystis polymorpha* Léger 1892: 113

1899 *Hirmocystis polymorpha* Labbé 1899: 13

1903 *Eirmocystis polymorpha* Minchin 1903: 197, 335

1911 *Hirmocystis polymorpha* Wellmer 1911: 123

Sporonts in associations of from two to twelve, arranged linearly or bi- or tri-furcate, largest individuals always at anterior end of chain. Length sporonts 100 to 150 μ , whole series attaining 1½ mm. Ratio LP:TL: :1:6 to 8; WP:WD: :1:1. First protomerite rounded at apex, wider than high, constriction at septum. Deutomerite elongate cylindrical, truncate at extremity. Epimerite a simple cylindrical knob. Nucleus spherical, one karyosome.

Cysts spherical, 100 μ . Dehiscence by rupture, spores ovoidal, 11 by 5 μ . Intestine of *Limnobia* sp., larva; *Systemocerus caraboides* L. larva. Taken in Poitou, France and in East Prussia.

Family ACTINOCEPHALIDAE Léger 1892: 166

Genus ACTINOCEPHALUS Stein 1848: 196

ACTINOCEPHALUS TIPULAE (Hammerschmidt) Léger
[Figure 6]

1838	<i>Bullulina Tipulae</i>	Hammerschmidt	1838: 357
1846	<i>Gregarina Tipulae</i>	Frantzius	1846: 28
1851	<i>Gregarina Tipulae</i>	Diesing	1851: 16
1859	<i>Gregarina Tipulae</i>	Diesing	1859: 739
1863	<i>Gregarina Tipulae</i>	Lankester	1863: 94
1892	<i>Actinocephalus tipulae</i>	Léger	1892: 141
1899	<i>Actinocephalus tipulae</i>	Labbé	1899: 26
1899	<i>Actinocephalus tipulae</i>	Léger	1899: 532
1903	<i>Actinocephalus tipulae</i>	Minchin	1903: 337
1911	<i>Actinocephalus tipulae</i>	Wellmer	1911: 130

Sporonts solitary, obese. Length nearly a millimeter. Width not given. Ratio LP:TL: :1:3.5 to 5; WP:WD: :1:1. Protomerite sub-spherical, widest in middle, deeply constricted at septum. Deutomerite widest at shoulder and tapers from thence to a rather short sharply pointed extremity. Epimerite not seen when alive and penetrating a cell, hence its supposed digitiform appendages not delineated. Portion seen a large round apically pointed papilla superimposed upon a short thick neck. Nucleus large, spherical. Several karyosomes.

Cysts spherical, 250 to 300 μ spores fusiform, 9 by 4 μ .

Intestine of *Tipula oleracea* L., larva, *Pachyrhina pratensis*, larva.

Taken in the Valley of the Vienne, France, and in East Prussia.

Diesing credits Hammerschmidt with having first seen and named this species. Since no data whatever exists concerning the species until Legér's time, it is doubtful that the two species are identical, especially since *Tipula* is parasitized by several gregarines, but the old record stands. Diesing gives as host *Ctenophora pectinicornis*, larva, in body cavity.

Léger places the species positively in the genus stated:

Ces caractères, (the epimerite as described above) joints à ceux fournis par la forme du sporadin du kyste et des spores, font rentrer, sans aucun doute, cette Grégarine dans le genre *Actinocephalus*.

ACTINOCEPHALUS sp. Léger

1899	<i>Actinocephalus</i> sp.	Léger	1899: 532
1903	? <i>Actinocephalus</i> sp.	Minchin	1903: 333

Host: *Ctenophora* sp., larva.

This species is not described, but merely mentioned in a list of other species found by Léger.

Genus SCHNEIDERIA Léger 1892: 153

Sporonts solitary. Protomerite separated from deutomerite by constriction but no septum (pseudomonocystid). Epimerite a flat disc with milled border, with or without central spine. Cyst dehiscence by simple rupture. Spores biconical, smooth. (It might be possible that a septum exists in the young trophozoites although this is not suggested by Léger.)

SCHNEIDERIA CAUDATA (von Siebold) Léger

[Figures 4 and 5]

1839	<i>Gregarina caudata</i>	von Siebold	1839: 51
1845	<i>Gregarina caudata</i>	Dujardin	1845: 638
1846	<i>Gregarina caudata</i>	Frantzius	1846: 23
1848	<i>Actinocephalus caudatus</i>	Frantzius	1848: 195
1851	<i>Gregarina caudata</i>	Diesing	1851: 8
1859	<i>Gregarina caudata</i>	Diesing	1859: 729
1863	<i>Gregarina caudata</i>	Lankester	1863: 94
1875	<i>Gregarina caudata</i>	Schneider	1875: 591
1892	<i>Schneideria coronata</i>	Léger	1892: 155
1899	<i>Schneideria caudata</i>	Labbé	1899: 22
1903	<i>Schneideria caudata</i>	Minchin	1903: 337, 199

Sporonts solitary, elongate. Maximum length 1 mm. Ratio LP:TL: : 1:9; WP:WD: :1.1 :1. Protomerite flattened at apex, wider than high, widest in middle, constricted considerably to meet deutomerite but no septum present. Deutomerite long, slender, tapering from anterior end, a very long conical extremity. Epimerite a flattened disc with a milled border, no style in center, as in *S. mucronata*. Nucleus slightly ellipsoidal, one large karyosome.

Cysts not seen. Spores 20 by 10 μ .

Intestinal caeca of *Sciara nitidicollis* Meig., larva.

Taken in Poitou, France.

This parasite is one-fifth the length of its host, and because of the transparency of the host can easily be seen from without when both are alive.

No clue to the actual identity of this parasite exists in the earlier work except this by Diesing (1851):

Proboscis brevissime cylindrica apice subglobosa truncata crenata, uncinis retractus? which seems to apply to the epimerite. It seems strange, if this species is meant, that no one mentions the absence of a septum until Léger described anew the species with a new name. He does not refer to the earlier workers.

Labbé, however, unites the species under the older name. The hosts are identical.

SCHNEIDERIA MUCRONATA Léger Type species
[Figures 1, 2 and 3]

1892	<i>Schneideria mucronata</i>	Léger	1892: 153
1899	<i>Schneideria mucronata</i>	Labbé	1899: 22
1903	<i>Schneideria mucronata</i>	Minchin	1903: 199, 333

Sporonts solitary, elongate. Length 700–800 μ . Width not given. Ratio LP:TL: :1:7; WP:WD: :1:1. Protomerite irregularly triangular, pointed, widest two-thirds its length from the apex. Deep constriction between protomerite and deutomerite. No septum. Deutomerite slender, gradually tapering from anterior end to a long slender point. Epimerite a wide flattened disc with a milled border and a short style in the center. Nucleus large, spherical, one karyosome. Very agile in movement, also polymorphic.

Cysts 270 by 190 μ , fusiform spores 15 by 9 μ .

Intestinal caeca of *Bibio marci* (L.), larva.

Taken in Tourraine and Poitou, France.

SCHNEIDERIA sp. Léger

1899	<i>Schneideria</i> sp.	Léger	1899: 526, 532
1903	<i>Schneideria</i> sp.	Minchin	1903: 333

Very briefly described as unilocular, less than 250 μ in length, greatly dilated in the anterior portion and gradually tapering posteriorly. Epimerite not seen. Judging by context from similar parasites in other fly larvae, the author considers it a Polycystid rather than a Monocystid, which it resembles.

Host: *Chironomus* sp., larva.

Taken in Poitou, France

Genus STYLOCYSTIS Léger 1899: 529

Dicystid gregarine with a simple epimerite in form of a sharply pointed recurved spine. Spores biconical.

STYLOCYSTIS PRAECOX Léger Type species

[Figure 33]

1899	<i>Stylocystis praecox</i>	Léger	1899: 529
1903	<i>Stylocystis praecox</i>	Minchin	1903: 199, 337
1911	<i>Stylocystis praecox</i>	Sokolow	1911: 283

Sporonts solitary, elongate, maximum length 500 μ , width not given. Ratio LP:TL: :1:10. WP:WD: :1:1. Body cylindrical, somewhat dilated in anterior end. Tapering slightly at posterior end, end blunt. Nucleus spherical with one karyosome. Epimerite a slender recurved pointed spine.

Cysts elongate-ovoidal, 200 μ in long axis. Spores biconical, 8 by 5 μ . Intestine of *Tanytus* sp., larva.

Taken at Grenoble, France.

Genus TAENIOCYSTIS Léger 1906: 307

Deutomerite of sporont divided by septa into numerous segments one behind the other. Epimerite a small sphere set with six or eight recurved hooks. Spores biconical.

TAENIOCYSTIS MIRA Léger Type species

[Figures 34 and 35]

1905?		Léger	1905: ?
1906	<i>Taeniocystis mira</i>	Léger	1906: 307
1908	<i>Taeniocystis mira</i>	Léger and Duboscq	1908a: 105
1911	<i>Taeniocystis mira</i>	Sokolow	1911: 284
1913	<i>Taeniocystis mira</i>	Ellis	1913: 280

Sporonts solitary, elongate cylindrical, deutomerite segmented, superficially resembling a tapeworm. Length 400–500 μ . Width not given. Ratio LP:TL: :1:11. WP:WD: :1:1. Epimerite a relatively very small bulb with a corona of 6 to 8 recurved hooks set upon a short neck.

Cysts spherical, 130 μ , spores 7 by 3 μ .

Host: *Ceratopogon solstitialis* Winn., larva.

Taken at Cavaliere, France.

Genus PILEOCEPHALUS Schneider 1875: 591

Epimerite a small lance-shaped or simple conoidal papilla placed unstalked upon the protomerite. Spores biconical.

PILEOCEPHALUS STRIATUS Léger and Duboscq

[Figure 100]

1909	<i>Pileocephalus striatus</i>	Léger and Duboscq	1909b: 887
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Sporonts solitary, length 150 μ . Protomerite more or less hemispherical, deutomerite broad, obtusely pointed. Epimerite a long striated bulb upon a short stout neck. Nucleus large, spherical, often found in the

protomerite (a phenomenon which has been nowhere else except in the species *Pileocephalus chinensis* by Schneider in 1886 and in *Acanthospora polymorpha* by Léger in 1897).

Cysts spherical.

Development extracellular, no cell destruction.

Intestine of *Ptychoptera contaminata*, larva.

Taken in Belgium?

LIST OF SPECIES FOUND IN THE ORDER SIPHONAPTERA OF
THE CLASS HEXAPODA

PARASITE	Host
ACTINOCEPHALIDAE	
<i>Actinocephalus parvus</i> Wellmer	<i>Ceratopsyllus fringillae</i> (Wlk.)
	<i>C. gallinae</i> (Schrank), larvae
<i>Steinina rotunda</i> Ashworth and Rettie	<i>Ceratopsyllus styx</i> Roths.
GENUS OF UNCERTAIN POSITION	
<i>Agrippina bona</i> Strick.	<i>Ceratophyllus fasciatus</i> Bosc. larv.

Family ACTINOCEPHALIDAE Léger 1892: 166

Genus ACTINOCEPHALUS Stein 1848: 196

ACTINOCEPHALUS PARVUS Wellmer

[Figures 114 and 120]

1911 *Actinocephalus parvus* Wellmer 1911: 131

Sporonts ovoidal, maximum dimensions 140μ by 75μ . Ratio LP:TL: : 1:5; WP:WD: :1:1.3. Nucleus ovoidal, several karyosomes. Epimerite a corona of eight digitiform processes situated upon a short neck.

Cyst and spores unknown.

Intestine of *Ceratopsyllus fringillae* (Wlk.), larva (*Ceratophyllus f.*); and *C. gallinae* (Schrank), larva.

Taken at Königsberg.

Genus STEININA Léger and Duboscq 1904: 352

Epimerite a short mobile digitiform process changing into a flat button. Spores biconical.

STEININA ROTUNDATA Ashworth and Rettie

[Figures 121, 122, 123 and 124]

1912 *Steinina rotundata* Ashworth and Rettie 1912: 31

Sporonts solitary, obese to pyriform. No constriction at septum. Maximum dimensions 180μ by 80μ . Nucleus spherical, one or two large karyosomes.

Cysts spherical, 110μ to 185μ in diameter. Dehiscence by simple rupture. Spores ovoidal, 12μ by 7μ . Extracellular development. Intestine of *Ceratopsyllus styx* Roths. (*Ceratophyllus s.*)

Taken near Edinburgh.

Genus of Uncertain Position

AGRIPPINA Strickland 1912: 108

Sporonts solitary, epimerite a circular disc armed with digitiform processes on periphery, a short neck. Spores ellipsoidal.

AGRIPPINA BONA Strickland 1912: 108 Type species

[Figures 101, 102, and 103]

1912 *Agrippina bona* Strickland 1912: 108

Sporonts elongate conoidal, average length 175 μ . Nucleus ellipsoidal. Protomerite dome-shaped, deutomerite tapering to a long pointed extremity from the shoulder. Epimerite as in genus.

Cysts spherical, dehiscing by rupture. Spores smooth, ellipsoidal, 6.6 by 7 μ .

Intestine of *Ceratophyllus fasciatus* Bosc., larva.

Taken at Cambridge, England.

LIST OF SPECIES FOUND IN THE SUBPHYLUM TUNICATA

PARASITE	Host	
[? Kölliker]	<i>Phallusia mamillaris</i> Ecker	
[? Ritter]	<i>Perophora annectens</i>	
[? Frenzel]	<i>Salpa maxima</i>	
[? Roboz]	<i>Salpa confoederata</i> , <i>S. vagina</i>	
[? Bargoni]	<i>Salpa aeruginosa</i>	
	[?Kölliker]	
	[Figure 55]	
1848 <i>Gregarina phallusiae</i>	Kölliker	1848: 35
1848 <i>Stylorhynchus Phallusiae</i>	Frantzius	1848: 195
1851 <i>Gregarina Phallusiae</i>	Diesing	1851: 9
1859 <i>Gregarina Phallusiae</i>	Diesing	1859: 728
1863 <i>Gregarina Phallusiae</i>	Lankester	1863: 95
1899 <i>Pleurozyga phallusiae</i>	Labbé	1899: 49
1903 <i>Pleurozyga phallusiae</i>	Minchin	1903: 339

The figure given by Kölliker indicates the presence of a septum. Animal solitary, length 30 to 40 μ . Ratio LP:TL: :1:4.5. WP:WD: :1:1. Protomerite dome-shaped, constricted at septum. Deutomerite cylindrical, tapering slightly and ending in a broad, rounded extremity. Nucleus spherical. Epimerite a short bulbous style.

Cyst and spores unknown.

Taken at Triest.

Intestine of *Phallusia mamillaris* Ecker.

The position of the gregarines in Tunicates is still uncertain. Little work has been done on them for thirty years and they offer an interesting

field from a phylogenetic point of view—both as regards the hosts and the parasites themselves. The Tunicates represent the highest type of hosts recorded for gregarines. Whether or not the gregarines are also the most complex is a problem of the future.

[? Ritter]
[Figure 98]

1893	<i>Gregarina</i> sp.	Ritter	1893: 69
1899	<i>Gregarina</i> sp.	Labbé	1899: 37
1903	<i>Gregarina</i> sp.	Minchin	1903: 339
1913	<i>Gregarina</i> sp.	Ellis	1913: 271, 290

40 μ in diameter. The parasites were found in the digestive tract, boring through the walls, and in the coelom. Three bands characterize all but the smallest, made up of "many elongated granules possibly cuticular in structure though they seem to take the stain."

Host: *Perophora annectens*.

The specimens described have little the character of polycystid gregarines (Fig. 98). There is a superficial resemblance to the genus *Taeniocystis*, but they possess no protomerite, and in one instance two nuclei are present, which leads to the hypothesis that they may belong to the genus *Haplozoon*.

[? Frenzel]
[Figures 39 and 117]

1885	<i>Gregarina Salpae</i>	Frenzel	1885: 565
1899	<i>Gregarina salpae</i>	Labbé	1899: 37
1903	" <i>Gregarina</i> " <i>salpae</i>	Minchin	1903: 339

Intestine of *Salpa maxima*.

[? Roboz]

1886	<i>Gregarina flava</i>	Roboz	1886: 1, 46
1899	<i>Gregarina flava</i>	Labbé	1899: 37
1903	" <i>Gregarina</i> " <i>flava</i>	Minchin	1903: 339

Intestine of *Salpa confederata*, *S. vagina*.

[? Bargoni]

1894	<i>Gregarina ensiformis</i>	Bargoni	1894: 44
1899	<i>Gregarina ensiformis</i>	Labbé	1899: 37
1903	" <i>Gregarina</i> " <i>ensiformis</i>	Minchin	1903: 339

Intestine of *Salpa aeruginosa*.

The following data is given, by Bargoni, concerning this species:

Sospettaí tratarsi di qualche parassita e particolarmente di una *Gregarina* avendone già altra, di forma però semilunare, ma molto simile pel contenuto giallognolo, avuta in esame dal Prof. Kleinenberg, che la trovò frequentemente parassita nella *Cydidpe* e nella *Alciopa*. Di questa nuova forma, che non va confusa colla *Gregarina flava* del Roboz da me potuta osservare una volta sola in *Salpa aeruginosa*, mi occuperò altra volta, accontentandomi pel momento di distinguerla col nome di *Gregarina ensiformis* n. sp.

LIST OF HOSTS WITH THEIR GREGARINE PARASITES

HOST	PARASITE
PLATYHELMINTHES	
<i>Geoplana backi</i>	<i>Rhynchocystis geoplanæ</i> Fuhrman
<i>G. amagensis</i>	<i>Rhynchocystis geoplanæ</i> Fuhrman
<i>Planaria</i> sp.	<i>Lankesteria</i> sp. Swarczewsky
<i>Polyporus sulphureus</i>	Gregarine form, Wellmer
<i>Sorocoelis</i> sp.	<i>Lankesteria</i> sp. Swarczewsky
ANNELIDA: Polychaeta	
<i>Capitella capitata</i>	<i>Ancora lutzii</i> Hasselmann
<i>Clymenella torquata</i>	<i>Microtaeniella clymenellæ</i> Calkins
<i>Glycera siphonostoma</i>	<i>Gonospora glyceræ</i> Pixell-Goodrich
" "	<i>Gonospora intestinalis</i> Pixell-Goodrich
" "	Three unnamed parasites Pixell-Goodrich
<i>Ophelia neglecta</i>	<i>Rhytidocystis heneguyi</i> deBeauchamp
<i>Pareudrilus pallidus</i>	<i>Monocystis pareudrili</i> Cognetti de Martiis
" "	<i>Rhynchocystis hessei</i> Cognetti de Martiis
<i>Polydora ciliata</i>	<i>Polyrhabdina polydoræ</i> Caullery and Mesnil
<i>Polydora socialis</i>	<i>Doliocystis</i> sp. Faria, Cunha and Fonseca
" "	<i>Selendium cruzi</i> Faria, Cunha and Fonseca
<i>Pygospionis selicornis</i>	<i>Polyrhabdina pygospionis</i> Caullery and Mesnil
<i>Rhinodrilus incertus</i>	<i>Monocystis thamnodrili</i> Cogn. de Martiis
<i>Scolecopsis fuliginosa</i>	<i>Polyrhabdina spionis</i> Caullery and Mesnil
<i>Spio martinensis</i>	<i>Polyrhabdina brasili</i> Caullery and Mesnil
ANNELIDA: Oligochaeta	
<i>Kynotus Pittarellii</i>	<i>Taeniocystis legeri</i> Cogn. de Martiis
<i>Lumbricus terrestris</i>	<i>Monocystis rostrata</i> Muslow
" "	<i>Monocystis catenata</i> Muslow
<i>Lumbricus variegatus</i>	<i>Spirocystis nidula</i> Léger and Dubosq
<i>Glossoscolex wiengreeni</i>	<i>Monocystis perforans</i> Pinto
ANNELIDA: Hirudinea	
<i>Glossiphonia complanata</i>	<i>Metamera schubergi</i> Duke
<i>Hemiclepsis marginata</i>	" "
ROTIFERA	
<i>Euchlanis dilatata</i>	<i>Monocystis minima</i> Konsuloff
<i>Salpina mucronata</i>	" "
ECHINODERMATA	
<i>Echinocardium cordatum</i>	<i>Lithocystis foliacea</i> Pixell-Goodrich
" "	<i>Urospora neapolitana</i> Pixell-Goodrich
" sp.	<i>Urospora echinocardii</i> Pixell-Goodrich
<i>Spatangus</i> sp.	<i>Urospora echinocardii</i> Pixell-Goodrich
<i>Synapta purpureus</i>	<i>Lithocystis microspora</i> Pixell-Goodrich
<i>Synapta galliennei</i>	<i>Urospora synaptæ</i> Cuenot
<i>Synapta digilata</i>	<i>Gonospora mercieri</i> Cuenot
MOLLUSCA	
<i>Cerithium vulgatum</i>	<i>Gonospora testiculi</i> Trébouffi

CRUSTACEA

<i>Ampelisca spinipes</i>	<i>Cephaloidophora ampelisca</i> Kamm
<i>Anaspides tasmaniae</i>	<i>Ganymedes anaspidis</i> Huxley
<i>Atyephyra desmaresti</i>	<i>Uradiophora cuenoti</i> Mercier
<i>Balanus amphitrite</i>	<i>Pyxinooides balani</i> Trégouboff
<i>Balanus eburneus</i>	<i>Pyxinooides balani</i> Trégouboff
“ “	Unnamed parasite, Buddington
<i>Eriphia spinifrons</i>	<i>Porospora legeri</i> deBeauchamp
<i>Gammarus marinus</i>	<i>Cephaloidophora maculata</i> Léger and Duboscq
<i>Libinia dubia</i>	<i>Cephaloidophora olivia</i> Kamm
<i>Nephrops norvegicus</i>	<i>Porospora nephropsis</i> Léger and Duboscq
<i>Portunus depurator</i>	<i>Porospora maraisi</i> Léger and Duboscq
<i>Pisa gibosii</i>	<i>Porospora pisae</i> Léger and Duboscq
<i>Talitrus saltator</i>	<i>Cephaloidophora talitri</i> Mercier
<i>Talorchestia longicornis</i>	<i>Cephaloidophora delphinia</i> Kamm
<i>Uca pugnax</i>	<i>Cephaloidophora nigrofusca</i> Kamm
<i>Uca pugilator</i>	

CHILOPODA

<i>Scolopendra heros</i>	<i>Amphorocephalus amphorellus</i> Ellis
“ <i>subspinipes</i>	<i>Nina indicia</i> Merton
“ sp.	<i>Echinomera magalhãesii</i> Kamm
“ sp.	<i>Seticephalus elegans</i> Kamm
“ sp.	<i>Gregarina brasiliensis</i> Pinto
<i>Scolopendrella</i> sp.	Gregarine form, Wellmer

DIPLOPODA

<i>Callipus lactarius</i>	<i>Stenophora lactaria</i> Watson
<i>Euryurus erythropygus</i>	<i>Stenophora diplocorpa</i> Watson
<i>Fontancrria coarctata</i>	<i>Stenophora caudata</i> Watson
<i>Orthomorpha coarctata</i>	<i>Stenophora elongata</i> Ellis
“ <i>gracilis</i>	<i>Stenophora robusta</i> Ellis
“ sp.	“ “
“ sp.	<i>Fonsecaia polymorpha</i> Pinto
<i>Parajulus impressus</i>	<i>Stenophora impressa</i> Watson
“ <i>venustus</i>	<i>Stenophora robusta</i> Ellis
“ sp.	<i>Stenophora cockerellae</i> Ellis
<i>Rhinocriscus pugio</i>	<i>Stenophora cunhai</i> Pinto
“ sp.	<i>Stenophora lutzii</i> Pinto
“ sp.	<i>Stenophora cruzi</i> Pinto
“ sp.	<i>Stenophora viannai</i> Pinto
“ sp.	<i>Stenophora umbilicata</i> Pinto
“ sp.	<i>Stenophora tenuicollis</i> Pinto

THYSANURA

<i>Sminthurus fuscus</i>	Gregarine form, Wellmer
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ORTHOPTERA

<i>Ceuthophilus latens</i>	<i>Gregarina longiducta</i> Ellis
“ <i>maculatus</i>	<i>Gregarina longiducta</i> Ellis
“ <i>neglectus</i>	<i>Gregarina neglecta</i> Watson
“ <i>stygius</i>	<i>Gregarina stygia</i> Watson
“ <i>valgus</i>	<i>Gregarina consobrina</i> Ellis

<i>Conocephalus frater</i>	<i>Gregarina chagasi</i> Pinto
<i>Encopitophus sordidus</i>	<i>Gregarina nigra</i> Watson
<i>Forficularia auricularia</i>	Gregarine form, Pantel
<i>Gryllus abbreviatus</i>	<i>Gregarina galliveri</i> Watson
<i>Ischnoptera pennsylvanicus</i>	<i>Gregarina illinensis</i> Watson
<i>Melanoplus differentialis</i> *	<i>Gregarina nigra</i> Watson
“ <i>femur-rubrum</i>	“ “
<i>Udeopsyllae nigra</i>	<i>Gregarina udeopsyllae</i> Watson
HEMIPTERA	
<i>Spiniger</i> sp.	<i>Schizocystis spiniger</i> Machado
NEUROPTERA	
Aeschnidae lv.	<i>Bothriopsis claviformis</i> Pinto
<i>Aeschna</i> sp.	<i>Actinocephalus brachydactylus</i> Ellis
<i>Phryganea grandis</i>	<i>Diplocystis phryganeae</i> Berg-von-Emme
<i>Sympetrum rubicundulum</i>	<i>Prismatospora evansi</i> Ellis
<i>Tramea lacerata</i>	“ “
DIPTERA	
<i>Anopheles bifurcatus</i> lv.	<i>Cauleryella anophelis</i> Hesse
<i>Aphiochaeta rufipes</i> lv.	“ <i>aphiochaetae</i> Keilin
<i>Ceratophyllus fasciatus</i>	<i>Agrippina bona</i> Strickland
<i>Ceratopsyllus farreni</i>	<i>Steinina rotundata</i> Ashworth and Rettie
“ <i>fringillae</i> lv.	<i>Actinocephalus parvus</i> Wellmer
“ <i>gallinae</i> lv.	<i>Actinocephalus parvus</i> Wellmer
“ “ ad.	<i>Steinina rotundata</i> Ashworth and Rettie
“ <i>styx</i>	“ “
<i>Ficalbia doszeini</i> lv.	Unnamed par. Guenther
<i>Simulium bracteatum</i> lv.	Unnamed par. Strickland
<i>Stegomyia fasciata</i> lv.	<i>Lankesteria culicis</i> Stevenson and Wenyon
COLEOPTERA	
<i>Alobates pennsylvanicus</i>	<i>Actinocephalus zophus</i> Ellis
<i>Amara angustata</i>	<i>Steinina rotunda</i> Watson
<i>Asida opaca</i>	<i>Stylocephalus giganteus</i> Ellis
<i>Asida</i> sp.	<i>Stylocephalus giganteus</i> Ellis
<i>Brosicus cephalotes</i>	<i>Gregarina erecta</i> Wellmer
<i>Carabus</i> sp.	<i>Comeloides</i> sp. Wellmer
<i>Clerid</i> lv.	<i>Bulbocephalus wardi</i> Watson
<i>Coccinella</i> sp.	<i>Gregarina fragilis</i> Watson
“ sp.	<i>Gregarina katherina</i> Watson
<i>Coccinella novemnotata</i>	“ “
<i>Coptotomus interrogatus</i>	<i>Gregarina globosa</i> Watson
“ “	<i>Gregarina coptotomi</i> Watson
<i>Crypticus quisquilius</i>	<i>Gregarina ovoidea</i> Wellmer
<i>Cucujus</i> lv.	<i>Bulbocephalus elongatus</i> Watson
<i>Cychnus rostratus</i>	Gregarine form, Wellmer
<i>Dermestes lardarius</i>	<i>Pyxinia bulbifera</i> Watson
<i>Diabrotica vittata</i>	<i>Gregarina diabrotica</i> Kamm
Elateridae lv.	<i>Gregarina gracilis</i> Watson
<i>Eleodes</i> sp.	<i>Stylocephalus giganteus</i> Ellis
<i>Eusattus</i> sp.	“ “

<i>Harpalus aeneus</i>	<i>Gregarina polyaulia</i> Wellmer
<i>Harpalus pennsylvanicus</i>	<i>Actinocephalus gimbeli</i> Watson
“ “	* <i>erythropus</i> <i>Hirmocystis harpali</i> Watson
“ “	<i>longior</i> <i>Steinina harpali</i> Watson
<i>Harpalus ruficornis</i>	<i>Gregarina polyaulia</i> Wellmer
<i>Heledona agricola</i>	Gregarine form, Wellmer
<i>Helophorus aquaticus</i>	<i>Monocystis</i> sp. Wellmer
<i>Hydrophilus aterrimus</i> lv.	Cometoides-like form, Wellmer
“ sp.	<i>Bothriopsis terpsichorella</i> Ellis
<i>Hylobius abietis</i>	<i>Gregarina hylobii</i> Kamm
<i>Ips typographus</i>	<i>Gregarina typographi</i> Fuchs
<i>Lagriia hirta</i>	<i>Gregarina rostrata</i> Wellmer
<i>Leptochirus edax</i>	<i>Actinocephalus crassus</i> Ellis
“ “	<i>Stylocystis ensiferus</i> Ellis
<i>Ninus interstitialis</i>	<i>Gregarina guatemalensis</i> Ellis
<i>Nyctotheres barbarata</i>	<i>Actinocephalus zophus</i> Ellis
<i>Omoplata normalis</i>	<i>Gregarina watsoni</i> Pinto
<i>Platydema excavatum</i>	<i>Gregarina platydema</i> Kamm
<i>Platynus ruficollis</i>	<i>Gregarina platyni</i> Watson
<i>Procrustes coriaceus</i>	<i>Actinocephalus permagnus</i> Wellmer
<i>Pterostichus niger</i>	<i>Gregarina exiguus</i> Kamm
“ “	<i>Actinocephalus echinatus</i> Wellmer
<i>Pterostichus stygicus</i>	<i>Gregarina monarchia</i> Watson
“ “	<i>Gregarina intestinalis</i> Watson
“ <i>vulgaris</i>	<i>Actinocephalus echinatus</i> Wellmer
<i>Systema</i> sp.	<i>Gregarina aragai</i> Pinto
<i>Tenebrio castaneus</i>	<i>Gregarina grisea</i> Ellis
Tenebrionidae lv.	<i>Gregarina tenebrionella</i> Watson
<i>Tribolium ferrugineum</i>	<i>Gregarina minuta</i> Ishii
“ “	<i>Gregarina crassa</i> Watson
“ “	<i>Didymophyes minuta</i> Kamm
“ “	<i>Steinina obconica</i> Ishii
<i>Tritoma quadripustulata</i>	Gregarine form, Wellmer
LEPIDOPTERA	
<i>Endrosia fenestrella</i> lv.	<i>Leidyana tinei</i> Keilin
<i>Oecophora pseudopretella</i>	Unnamed Gregarine
<i>Tinea pallescentella</i>	Unnamed Gregarine
ARACHNIDA	
<i>Ctenocephelus serraticeps</i>	<i>Gregarina ctenocephalus</i> Ross
<i>Oribata geniculata</i>	<i>Gregarina</i> sp. Wellmer
TUNICATA	
<i>Stolonica socialis</i>	<i>Selysina perforans</i> Duboscq
ENTEROPNEUSTA	
<i>Glossobalanus minutus</i>	<i>Selenidium metchnikovi</i> Léger and Duboscq

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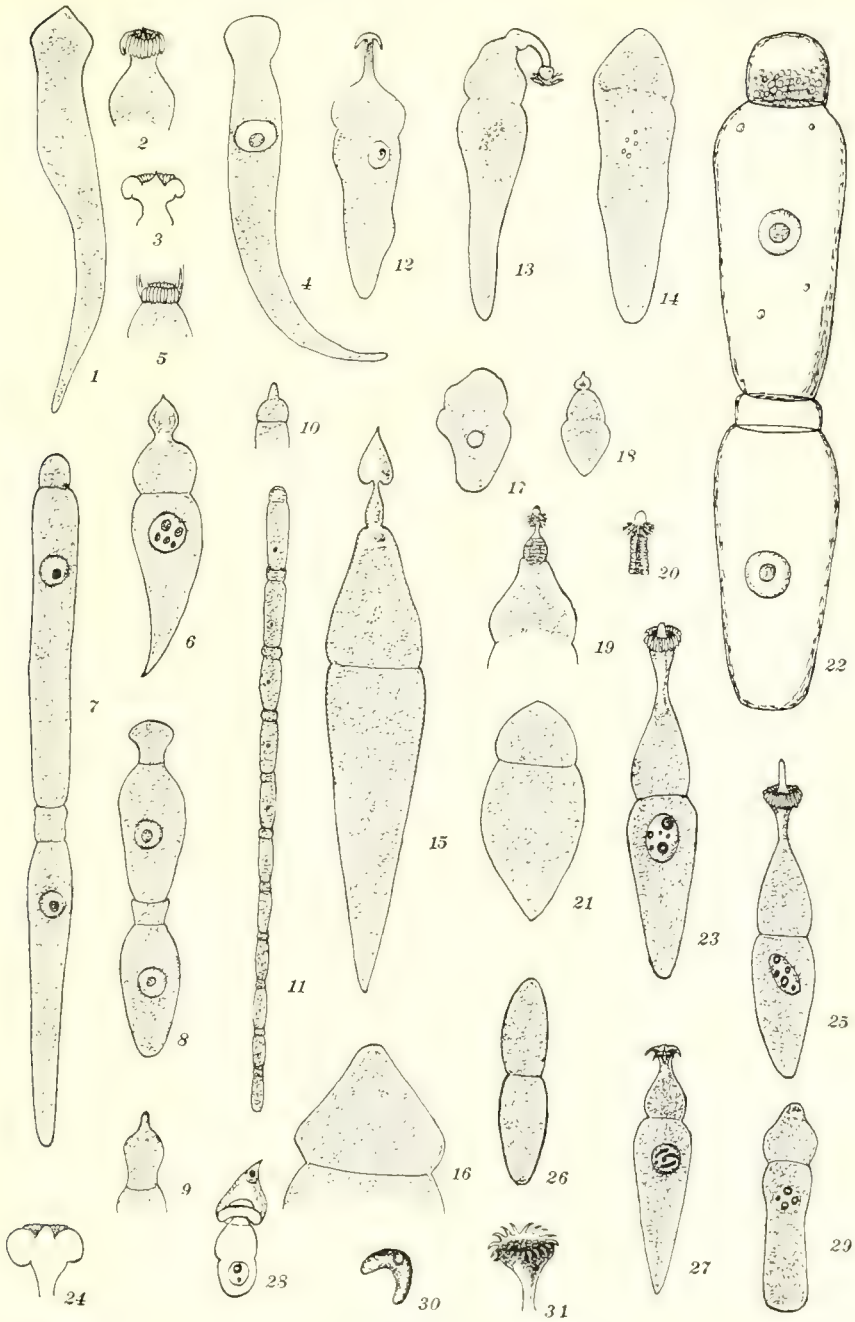
EXPLANATION OF PLATES

Drawings were either traced directly from the author's plates or enlarged by means of the camera lucida. Magnifications are not given for they did not appear in most of the original sources. The text will furnish the exact size of each species so far as data were available in the original publication or in the later articles.

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KAMM

STUDIES ON GREGARINES II

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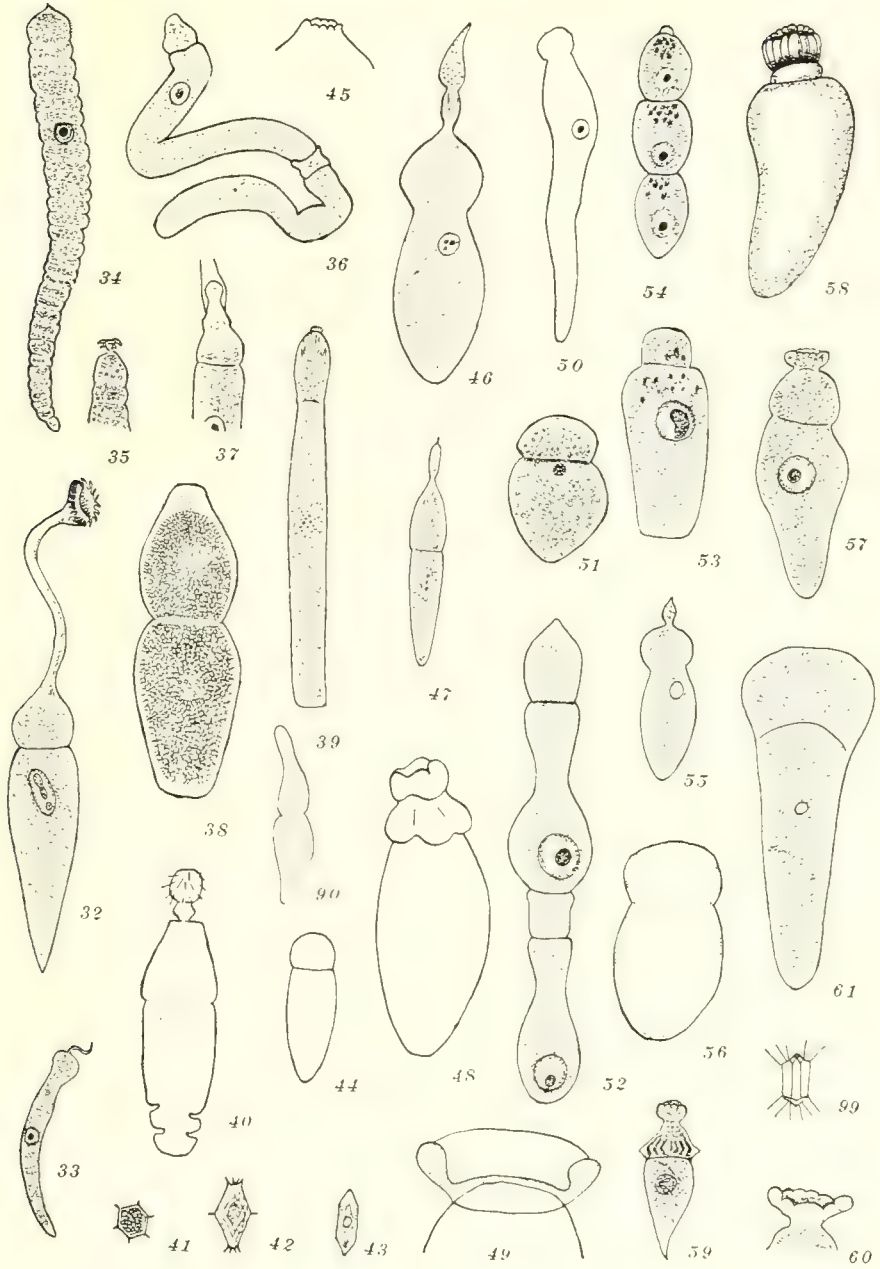


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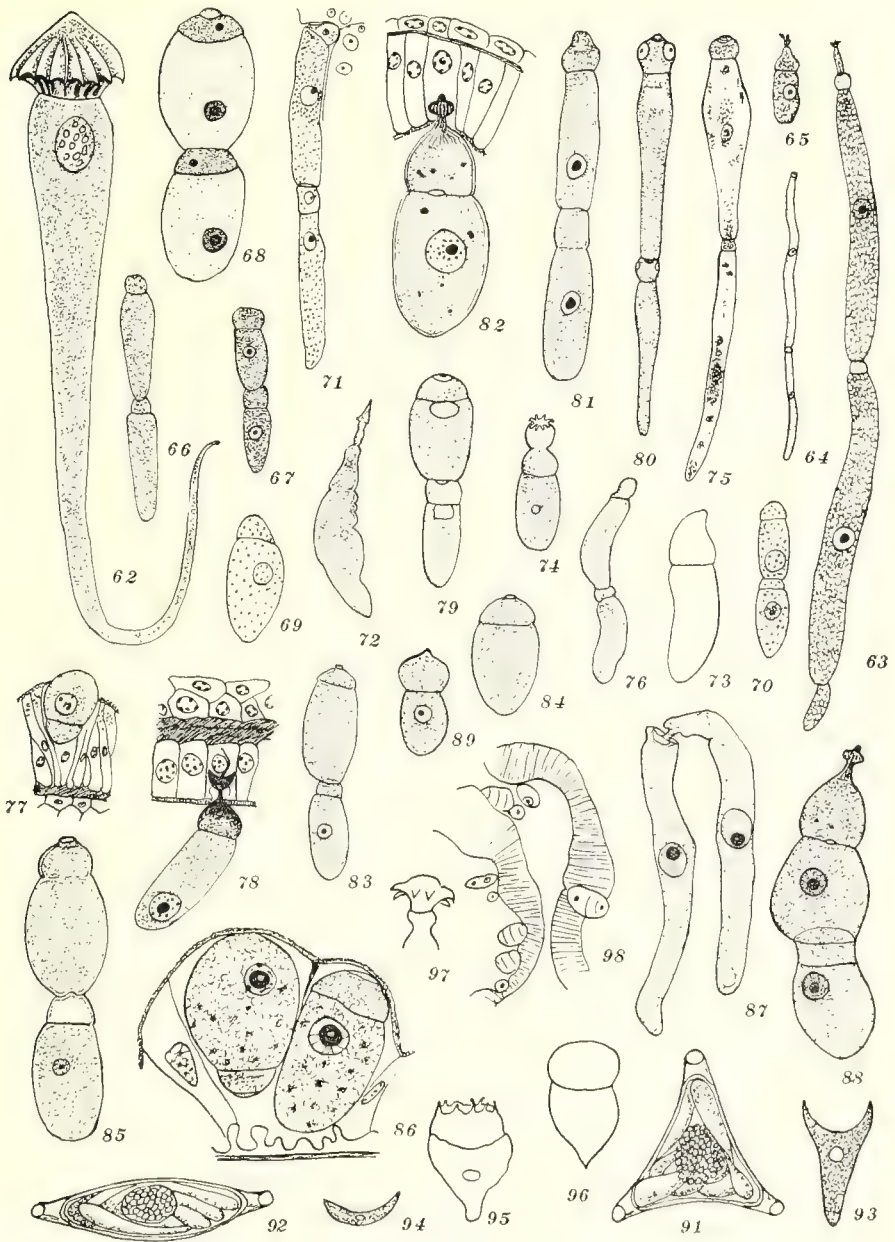
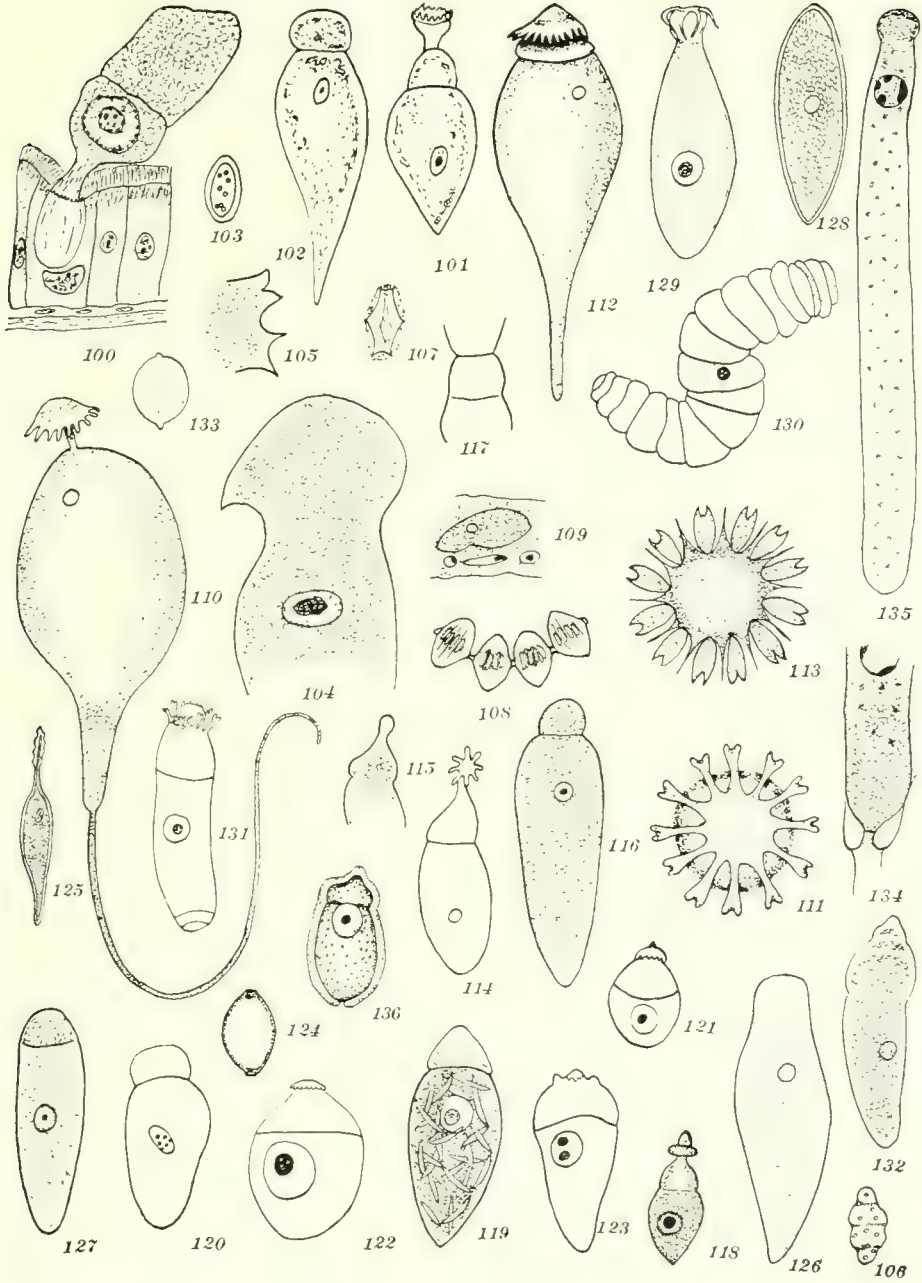


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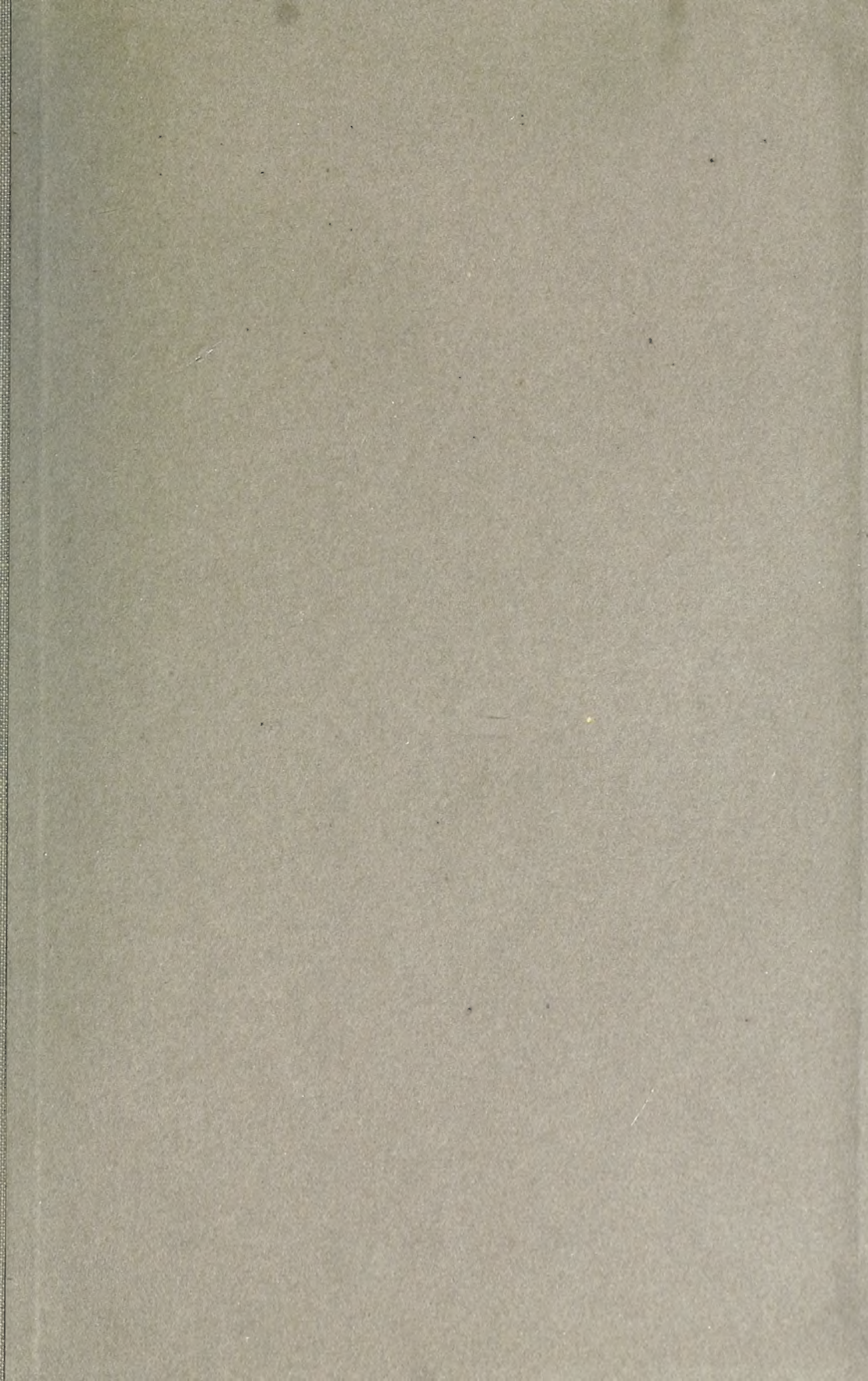
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